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THE LIVING BIRD

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THE LIVING BIRD

SEVENTEENTH ANNUAL

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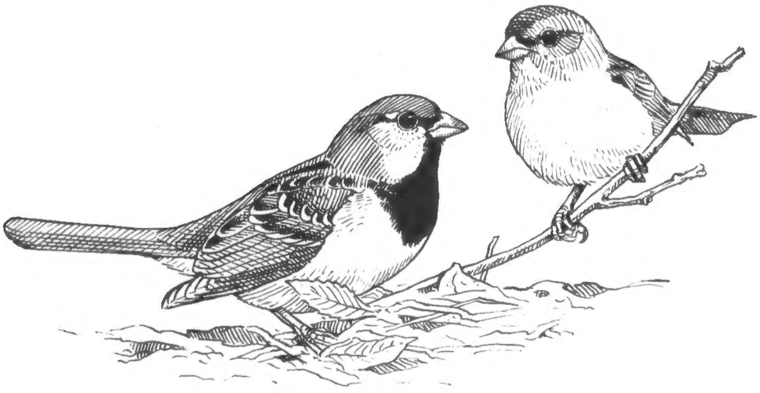

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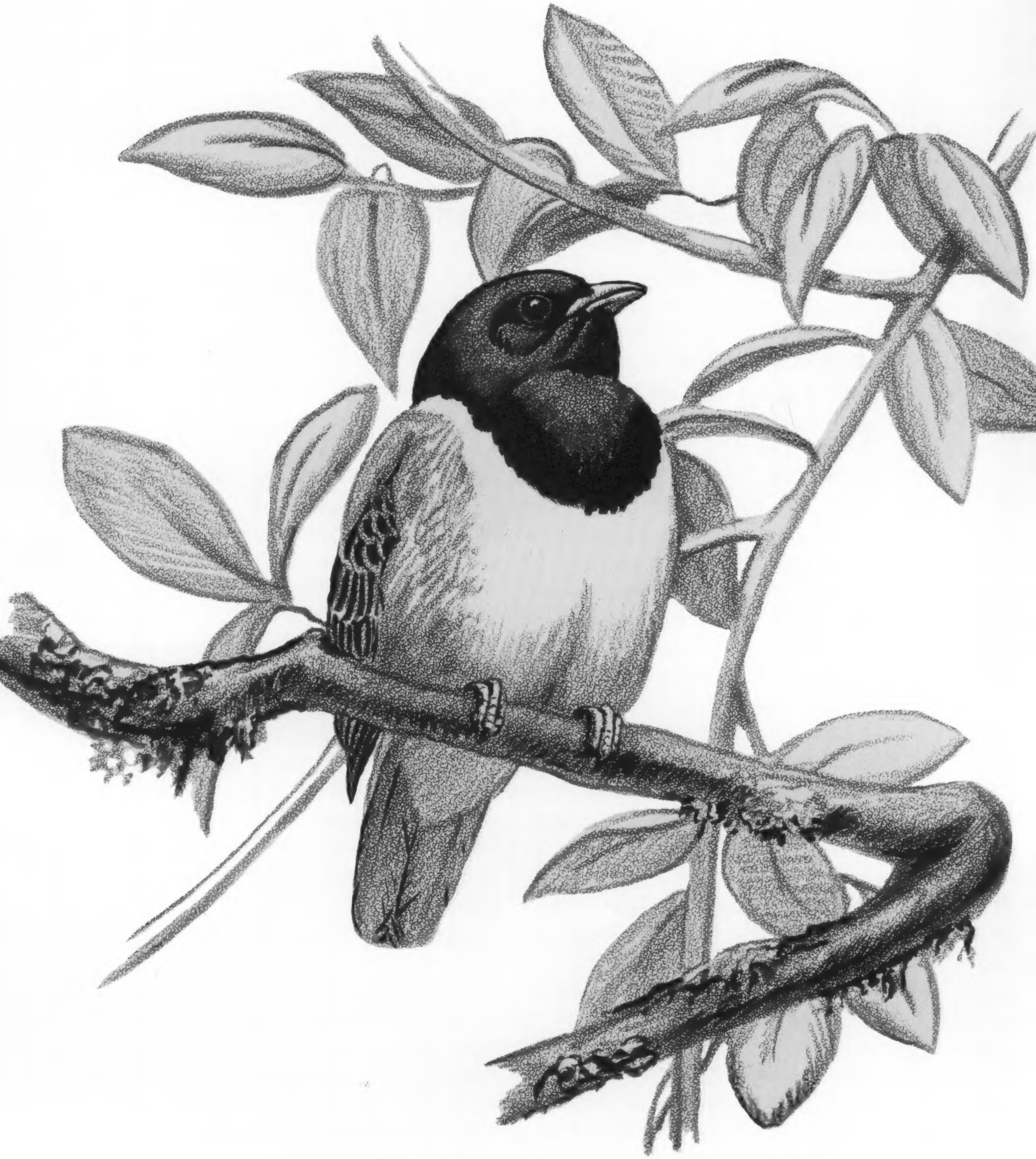

Green-and-black Fruiteater, *Pipreola riefferii*. Drawing by James E. Coe.

CONTENTS

THREE PINE GROSBEAKS. *George Miksch Sutton* 5

RED PHALAROPES BREEDING ON BATHURST ISLAND. *Harold F. Mayfield* 7

BEGGING BY NESTLING SHINY COWBIRDS: ADAPTIVE OR MALADAPTIVE. *Michael Gochfeld* 41

DISPLAY AND RELATED BEHAVIOR OF THE WIRE-TAILED MANAKIN. *Paul Schwartz* and *David W. Snow* 51

BEHAVIORAL INTERACTIONS AND NICHE SEPARATION IN BLACK AND TURKEY VULTURES. *Paul A. Stewart* 79

SOCIAL BEHAVIOR OF THE AFRICAN COMB DUCK. *W. Roy Siegfried* 85

A REVIEW OF THE HORNBILLS: BIOLOGY AND RADIATION. *Alan C. Kemp* ... 105

BREEDING ECOLOGY OF THE CLAY-COLORED SPARROW. *Richard W. Knapton* 137

THE COMMUNAL SOCIAL SYSTEM OF THE GREEN WOODHOOPOE IN KENYA. *J. David Ligon* and *Sandra Ligon* 159

ORGANIZATION OF A TROPICAL NECTAR FEEDING BIRD GUILD IN A VARIABLE ENVIRONMENT. *Jean-Luc DesGranges* 199

A NESTING STUDY OF THE BROWN CREEPER. *Cheyleen M. Davis* 237

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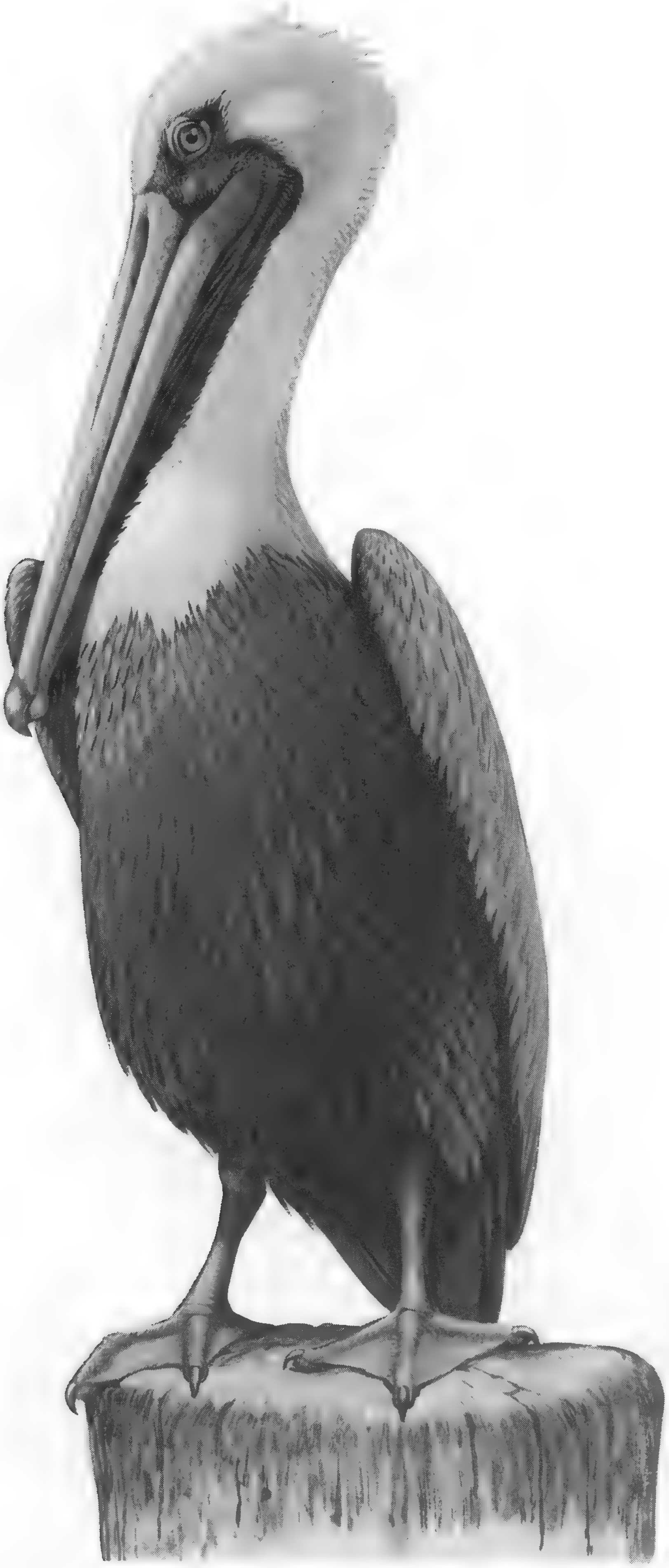
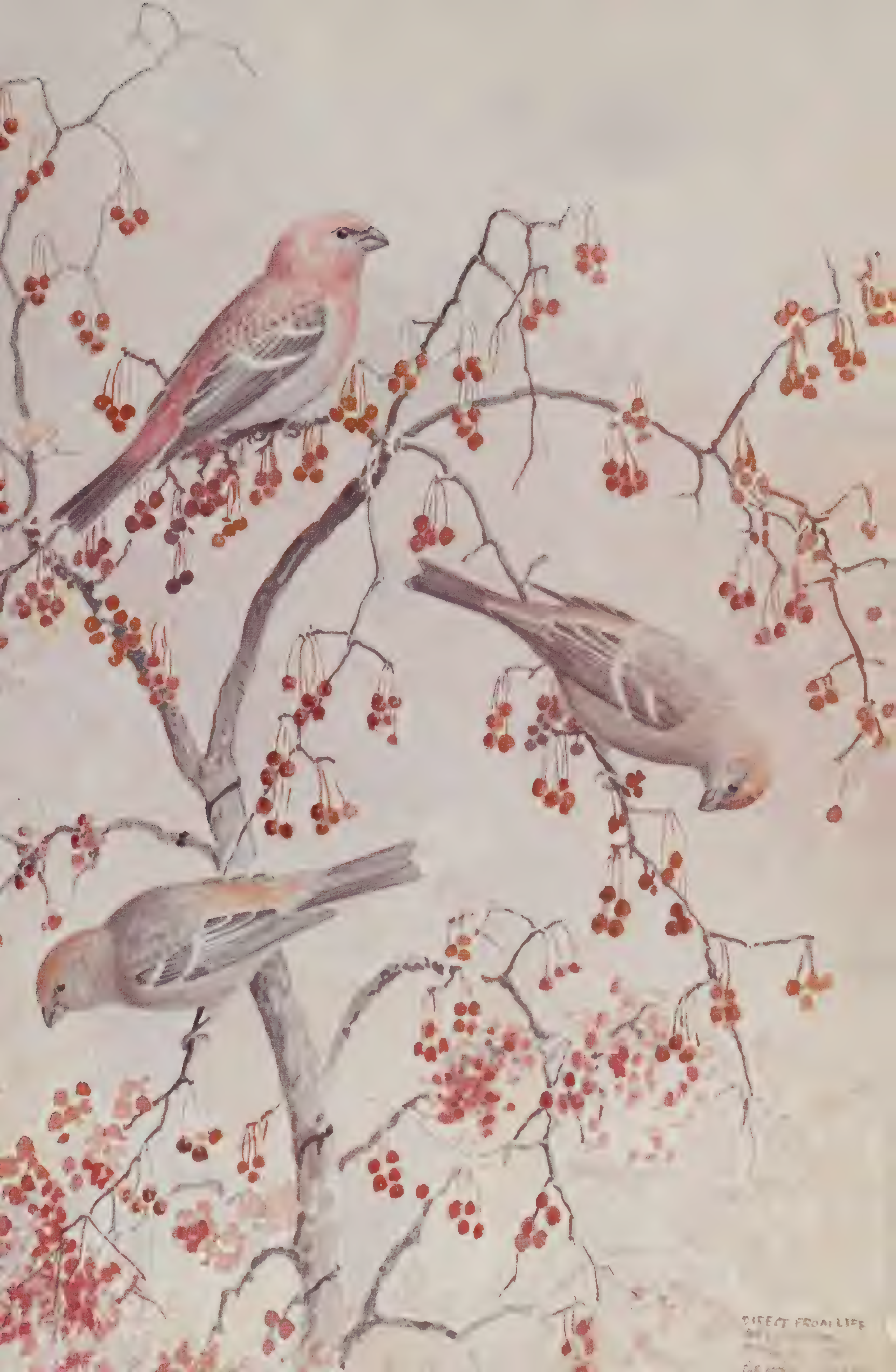


Brown Pelican, *Pelecanus occidentalis*. Drawing by Chuck Ripper.


DIRECT FROM LIFE

THREE PINE GROSBEAKS

George Miksch Sutton

When I consider how much time I have spent in wooded parts of the New World's North Country, I find it hard to believe that I have seen so little of the Pine Grosbeak *(Pinicola enucleator)* on its breeding ground. As a member of W. E. Clyde Todd's expedition down the Labrador in the summer of 1920, I did not expect to see the species, for I knew that that coast was virtually treeless; but while descending the Abitibi and the Moose by canoe in 1923, and the Missanaibi and the Moose in 1926, I expected to become well acquainted with it, for we were among conifers most of the time. The portage trails were lined with trees; yet hardly a Pine Grosbeak did we see or hear along those fine rivers. During the latter expedition I was to come upon the species unexpectedly at Richmond Gulf, at Lat. 56° 09′ N, on the east coast of Hudson Bay. There, on 10 August, among small but shapely spruces on a sheltered slope, I found a company of four birds, an adult female and her brood, the young all flying well and, so far as I could tell, not dependent on their parent for food. At Richmond Gulf the grosbeaks were at tree-limit, the northernmost edge of their habitat. Six years later, on 8 June, I was to find Pine Grosbeaks again at the north edge of their range, this time near the mouth of the Churchill River on the west coast of Hudson Bay, at Lat. 58° 45′ N. The two birds that I happened upon, a brightly colored male and his mate, were in a dense stand of fairly tall spruce through which the railroad's right-of-way had been cut. They were on their breeding ground: in the oviduct of the female specimen I found a fully formed egg. Needless to say, I looked hard for the nest, but did not find it.

In Alaska, in February and March of 1945, I was to see Pine Grosbeaks from time to time in the vicinity of Fairbanks. The birds were feeding on weed seeds, rose-hips, grain scattered along the roadside, and spruce and tamarack seeds (Sutton 1945, *Condor,* 47:267). According to my field notes, I heard full songs on 22 and 24 March, though the flock of 30 birds that I saw on the latter date contained no brightly colored adult males.

It was in Ann Arbor, Michigan, in 1951, that I truly became acquainted with the Pine Grosbeak. On 30 November of that year, Dale A. Zimmerman told me of "about a dozen" grosbeaks that he had just seen in the arboretum, not far from the main campus of the University of Michigan. The following day, Andrew J. Berger and I went looking for the handsome visitors. Not for some time did we find them, though we had made a point of going to the very spot at which they had been observed. They were surprisingly quiet while feeding; had one bird not uttered a low whistle as it changed perches, thus leading the others to move about a bit, we might never have found them. The eight or ten that we eventually saw gave low calls, mere whisperings, as they

---

Pine Grosbeaks, *Pinicola enucleator*. Painted from life by George Miksch Sutton. Courtesy of William Shepherd.

fed. They were unbelievably "tame." Two of them were literally within touching distance as they flew past us. Every bird was busy pulling off and chewing up tiny crab apples. Precisely what they were swallowing was difficult to say, for much of what they chewed at fell to the ground. Perhaps they were ingesting only the husked seeds. They were wonderfully "cozy" looking; the look on their faces was pensive; they appeared to be utterly unafraid, a little as if they'd never even seen human beings before.

That afternoon, armed with the old Fuertes paint-box and other equipment, I drew three of the grosbeaks direct from life. I had never done quite this sort of thing before. The birds were fine as models, for while they were chewing they did little else. Managing paper, paints, brushes, pencils, and erasers without easel or table was difficult. The birds that I elected to draw were a bright adult male and two females, or female-like individuals, the latter largely gray, with yellow-orange tones on head and rump. The white wing-bars were noticeable in all three.

A special memory of that afternoon is of the human passers-by. Many of these evidently sensed at a distance what I was up to, for they made a point of walking slowly and keeping well back. Not a single person waved or called or asked if he could come closer and watch. Each of them must have been curious, but not once did curiosity get the better of courtesy and understanding.

The painting, now owned by William M. Shepherd, Jr. of Little Rock, Arkansas, is the only one I have ever made direct from life of several wild, free-flying birds.

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RED PHALAROPES BREEDING ON BATHURST ISLAND

HAROLD F. MAYFIELD

The Red Phalarope *(Phalaropus fulicarius)* nests on Arctic islands and on the northernmost fringe of continental North America and Asia (Figure 1). At other seasons of the year it lives on southern seas, mainly south of the Equator in both hemispheres where ocean currents bring plankton to the surface in abundance (Meinertzhagen 1937:667; Murphy 1936:995; Stanford 1953:483). It is the most pelagic of the phalaropes and seldom comes onto land except when nesting. It nests farther north and winters farther south than the closely related Northern Phalarope *(Phalaropus lobatus)*, although their ranges overlap. The other member of the family, the Wilson's Phalarope *(P. tricolor)*, nests in the interior of North America and winters inland in South America.

The three species of phalaropes have attracted attention because of the reversal of usual sex roles. The females (Figure 2) are larger, more brightly colored, and more aggressive in courtship, and males provide the incubation of eggs and care of the young. The Red Phalarope has been studied least because of the remoteness of its nesting range. Most observations, except for those of Kistchinski (1975) and Schamel and Tracy (1977), have been limited to a single season or to incidental notes gathered in the course of other studies. This study offers more detailed information about the Red Phalarope's natural history than previously reported, and will hopefully encourage further study.

This account is based on three summers' field work on Bathurst Island in the Canadian Arctic: 22 June to 14 July 1970, 12 June to 20 July 1971, and 12 June to 17 July 1973. There I was a guest at the High Arctic Research Station of the National Museum of Natural Sciences (Canada). Important details, particularly the supplementary information for years before and after my visit, have been supplied by friends engaged in other projects at the Station.

Since the local population was small, I collected few specimens, and since the bird's tolerance of disturbance was unknown, I did not attempt to capture any for marking. Observation at nests took place mainly while concealed in a blind.

Habitat and the Avian Community

Bathurst Island lies near the center of the Canadian Arctic Archipelago (Figure 1). The greater part of the island is rolling upland. The hills, seldom rising above 300 meters are rounded from glaciation in the past, and the hilltops and slopes consist mainly of bare earth strewn with rock fragments and marked here and there with patches of thin vegetation — "saxifrage barrens."

The middle of the island is pinched between inlets from the east and west (Figure 3). Across this narrow waist stretches a low flat valley, Polar Bear Pass (Figure 4). The wet floor of this valley, mostly clothed in vegetation and dotted with freshwater ponds and lakes, contrasts sharply with the dry hills on either side. Its length is about 25 kilometers, its width about three km, and its elevation less than 25 meters above the sea. In the wettest and best vegetated portions of the valley floor, the Red Phalarope nested and fed (Figures 5 and 6), avoiding the hills and the narrow watercourses and scattered ponds among them.

The High Arctic Research Station overlooked Polar Bear Pass (Figure 4) from the north, situated on the brow of a hill about 14 km inland from Goodsir Inlet to the east, at Lat 75° 44′ N, Long 98° 25′ W.

At first glance the lowland looked like a golf course with many water hazards. But close-up, the turf proved to consist mostly of moss pierced by well spaced blades of sedge and grass. The leaves from the previous year often curled over at a height of about eight centimeters, giving an even surface almost as if mowed. The most prominent sedge was *Carex stans,* but several species of grasses were common also, especially *Arctagrostis latifolia* and *Eriophorum triste*.

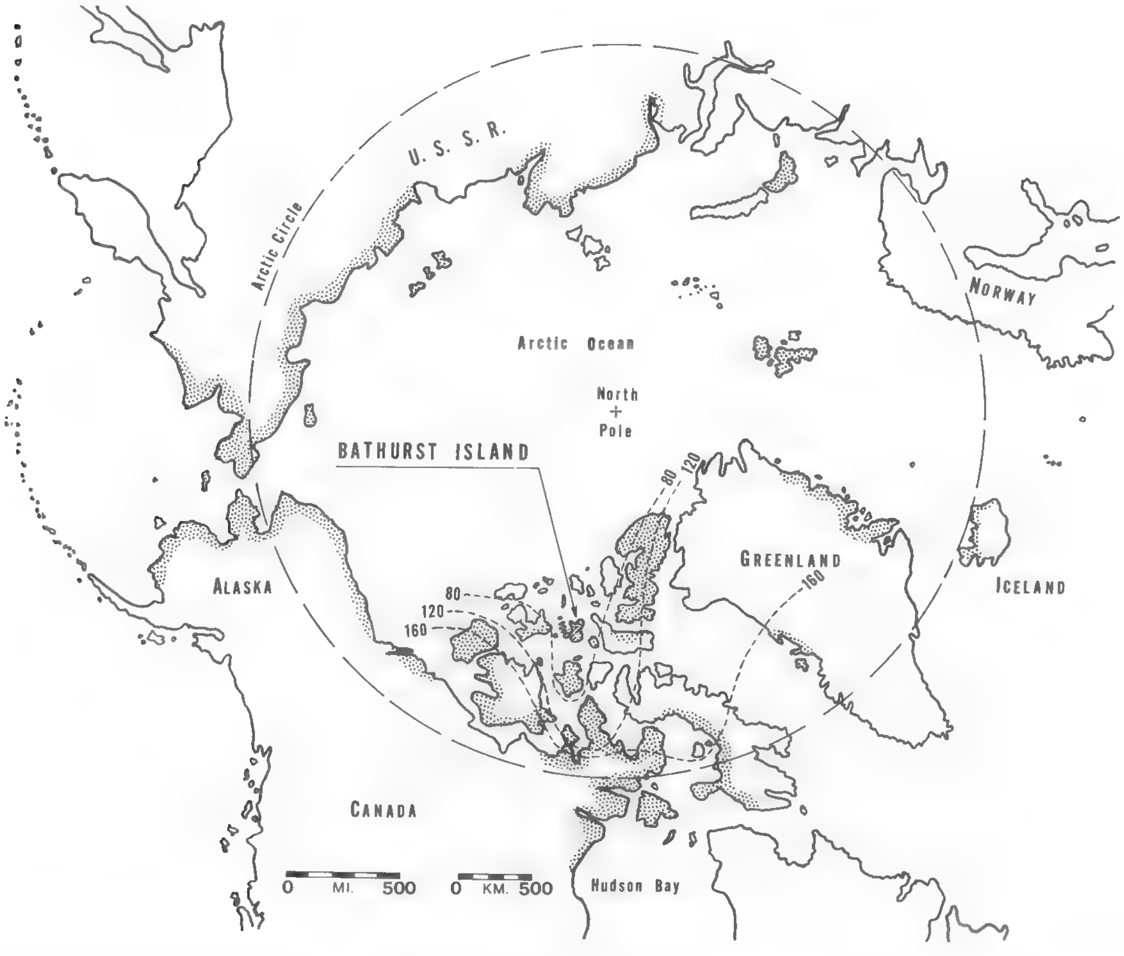


Figure 1. The Arctic. Stippling shows approximate breeding range of the Red Phalarope, mainly from Godfrey (1966:167) and Dement'ev (1969:289, 290). Dotted lines in the Canadian Arctic Archipelago show the "barren wedge" in flora, outlining the northern limits of zones supporting 160, 120, and 80 vascular plants (Beschel 1969:891). Bathurst Island lies within this zone of scanty vegetation and rigorous summer climate.

Adult phalaropes used the vegetation for concealment of nests and also for the food it harbored, and the young phalaropes hid under the vegetation and picked insects from it. Although the growth about some nests was scanty, the male phalarope enhanced the concealment by arching wisps of attached material over the eggs.

This choice of habitat is consistent with reports from other parts of the Arctic, where the common elements usually are wet grassy flats and freshwater ponds fed with melting snow (Kistchinski 1975:286–7). However, a few reports are curiously different. In Spitsbergen (Løvenskiold 1964:209) and on Seymour Island in the Canadian Arctic (Stewart D. MacDonald, pers. commun. 1975) Red Phalaropes have nested on islets without the usual vegetation and ponds. Perhaps an abundance of suitable food, which may be present on certain seashores, provides sufficient inducement for phalaropes to remain and nest.

Other birds present in the same area provide additional insight into the nesting situation. Nesting regularly on the tracts utilized by the phalaropes were the following: Red-throated Loon, *Gavia stellata*; King Eider, *Somateria spectabilis*; Black-bellied Plover, *Pluvialis squatarola*; Sanderling, *Calidris alba*; Glaucous Gull, *Larus hyperboreus*; Pomarine Jaeger, *Stercorarius pomarinus*; Parasitic Jaeger, *S. parasiticus*; and Long-tailed Jaeger, *S. longicaudus*. The White-rumped Sandpiper, *C. fuscicollis*, and the Lapland Longspur, *Calcarius lapponicus*, were present every year but not always nesting.

Other birds visited the phalarope area frequently: Brant, *Branta bernicla*; Snow Goose, *Chen caerulescens*; Oldsquaw, *Clangula hyemalis*; Rock Ptarmigan, *Lagopus mutus*; Red Knot, *Calidris canutus*; Purple Sandpiper, *C. maritima*; Baird's Sandpiper, *C. bairdii*; Thayer's Gull, *Larus thayeri*; Arctic Tern, *Sterna paradisaea*; Snowy Owl, *Nyctea scandiaca*; and Snow Bunting, *Plectrophenax nivalis*.

Population

Density

My field work focused most intensively on a rectangular tract 2 × ½ km (1km^2) chosen because it seemed characteristic of the wet tundra habitat where phalaropes nested. Here the number of phalarope nests for seven years beginning in 1970 was 6, 14, 0, 7, 0, 2, 4; mean density, 4.9 nests/km^2. (Information on 1972 supplied by Pierre Lamothe, and on 1974, 1975, and 1976 by John Geale.)

To get a better idea of the density over a larger and more representative portion of the entire valley, I enlarged the rectangle under consideration to 20 km^2, which was not under intensive observation but was traversed to some extent several times a day by members of our party. Here in 1973, the second-best nesting year out of seven, John Geale and I estimated 32 nesting males, or 1.6 nesting males per km^2. On these flats, where birds were few and vegetation low, the numbers of phalaropes present could be estimated fairly accurately by repeated inspections without finding all the nests. We verified this by trials.

Viewed from a distance, all of this area looked favorable to phalaropes, since it was fairly level and dotted with ponds, but close inspection showed many parts to consist of nearly bare soil that was not utilized in any way by phalaropes. Much of the central portion of Polar Bear Pass was occupied by lakes and ponds, and the suitable nesting habitat dwindled toward each end; so judging from the amount of habitat and the number of birds seen, I concluded the total population of phalaropes in good years was of the order of 100. The largest number of females seen by any of our party (Pierre Lamothe) was 60 on 6 July 1971.

In two unfavorable years very few phalaropes were seen, and none nested in my study area. In the entire region, members of the Station party found two nests in 1972 (Pierre Lamothe) and three nests and two broods of young in 1974 (John Geale).

Farther south in the Canadian Arctic, where vegetation and presumably food are more abundant, Red Phalarope densities are much greater. On two tracts near Bowman Bay on southwestern Baffin Island, Soper (1940:20) estimated 7 and 15 pairs per square kilometer. At Cambridge Bay on Victoria Island, Parmelee (letter dated 30 January 1974) estimated 20 "pairs" per km^2, and on the extensive flats of Jenny Lind Island, 12 "pairs." On Southampton Island, Sutton (1932:151) reported "thousands of young" in the marshy region west of South Bay in late summer. Similarly, in Siberia on the southeastern part of the Taimyr Peninsula, the Red Phalarope is "the most plentiful shorebird species" (Dement'ev et al. 1969:292); on the Indigirka and Yana deltas and the north shore on the Chukotski Peninsula the Red Phalarope ranged in density from 0.5 to 2.0 "pairs" per hectare in good habitat (Kistchinski 1975:286); and in sedge-moss bogs of northeastern Yakutsk, 2 "pairs" per ha (Uspenski, 1963:64). These Siberian estimates may indicate remarkable concentrations of 50 to 100 males per km^2, but the units of area may be misleading if the best nesting areas are attenuated and discontinuous. On a favorable area near Barrow, Alaska, Schamel and Tracy (1977:314) found nest densities of 24 per km^2 in 1974 and 44 per km^2 in 1975.

Sex Ratio

I was unable to determine the absolute ratio of males to females but judged the disparity was not great. Counts were difficult because some males could not be distinguished from females at a distance or in poor light. Also the proportions fluctuated. At first there was an excess of females. Then many males dropped out of sight while sitting on nests. Later, other males arrived, some identifiable by gray in their underparts, and females began to depart. At this time the ratio tipped toward the males, which became heavily favored by mid-July when most females had left and the remaining adults were nearly all males with nests or broods.

Arrival on the Nesting Ground

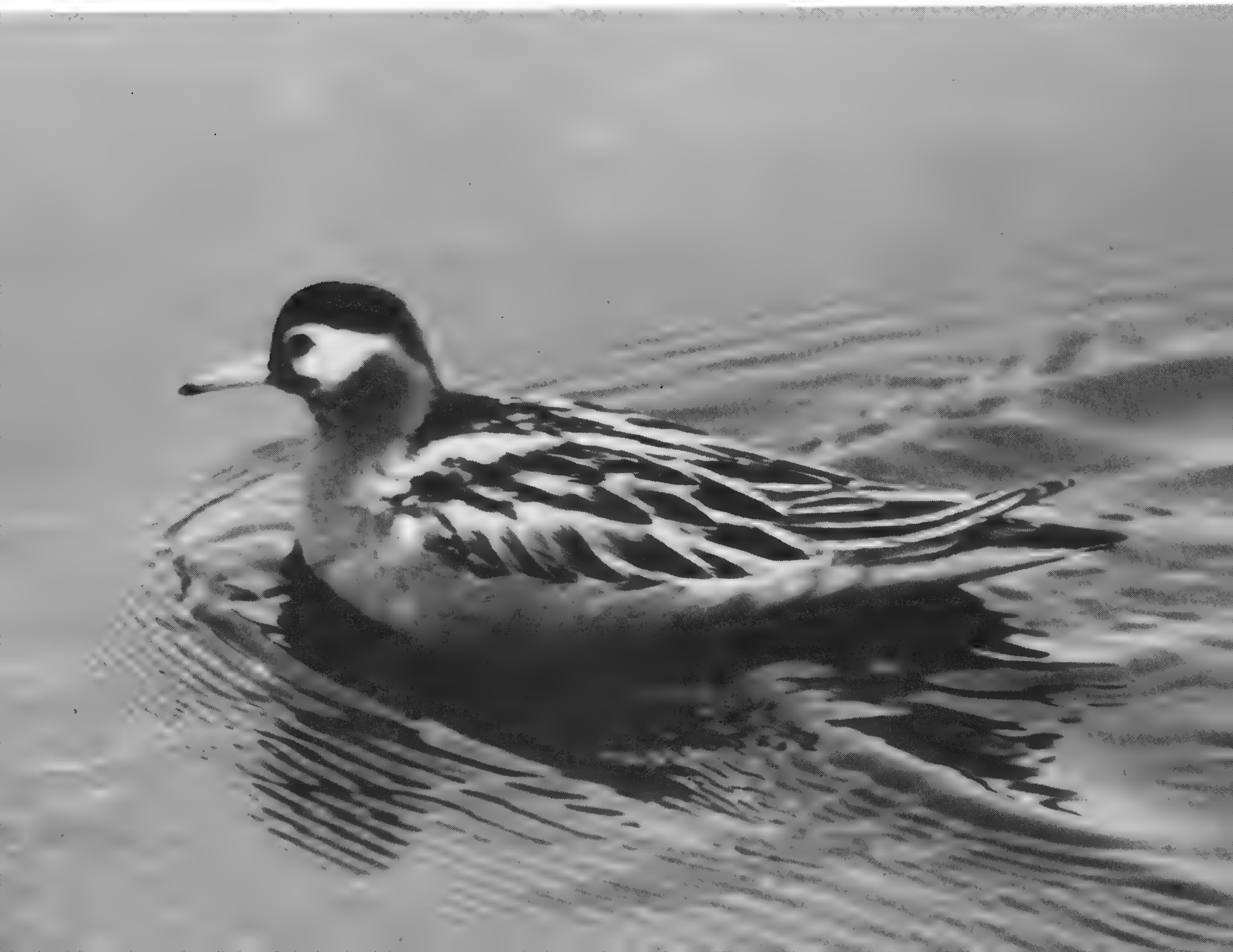
The Red Phalarope was the last of the nesting shorebirds to arrive on Bathurst Island, and even then arrivals were spread out over more than two weeks. The mean date of the first sightings for nine years, 1968 to 1977, was 16 June, with a range of 5 to 28 June. This was about two weeks later than Baird's Sandpiper, Red Knot, and Sanderling. Opposite the Canadian islands in Greenland, Salomonsen (1950:258) and Manniche (1910:14) also found the Red Phalarope to be the last of the spring arrivals, appearing there slightly before mid-June.

The Bathurst Island population probably comes from the Atlantic Ocean by way of Davis Strait and Baffin Bay. They are abundant at sea south and east of Greenland before and after the first of June (Wynne-Edwards 1935:295) and enter the bays of southeastern Baffin Island with the breakup of ice (Kumlien 1879:85). Migrants become numerous on shore at Frobisher Bay in the middle of June (Sutton and Parmelee 1951:215), and Wynne-Edwards (1952:370) saw large flocks flying past the capes northwest of Baffin Island about the same date. The spread through the nesting range is rapid, for the bird appears almost simultaneously at widely scattered points. Parmelee et al. (1967:137, 225) noted it at Cambridge Bay on southeastern Victoria Island on 11 June 1960 and 10 June 1962, and on Jenny Lind Island on 11 June 1966. These locations are about 800 km south of my study site.

It is possible the last leg of the migration to Bathurst Island is accomplished by long flight from the open sea. At this date the adjacent islands usually are surrounded by unbroken ice and their lands are covered with snow except for windswept hilltops and rivulets of meltwater, neither of which attracts phalaropes. No staging point is known for hundreds of kilometers on land or sea.

Usually the very first phalaropes to be seen on Bathurst Island appeared in a small portion of the valley where winter winds deposited dust from the hilltops and caused an early melt. Here marshy flats became available for feeding while the main nesting sites were still snow-covered. Various

Figure 2. The female Red Phalarope shows more contrast on the head and back than the male, her upperparts appearing nearly black and white in the field against the reddish brown of the underparts. Photograph by Ralph Palmer.



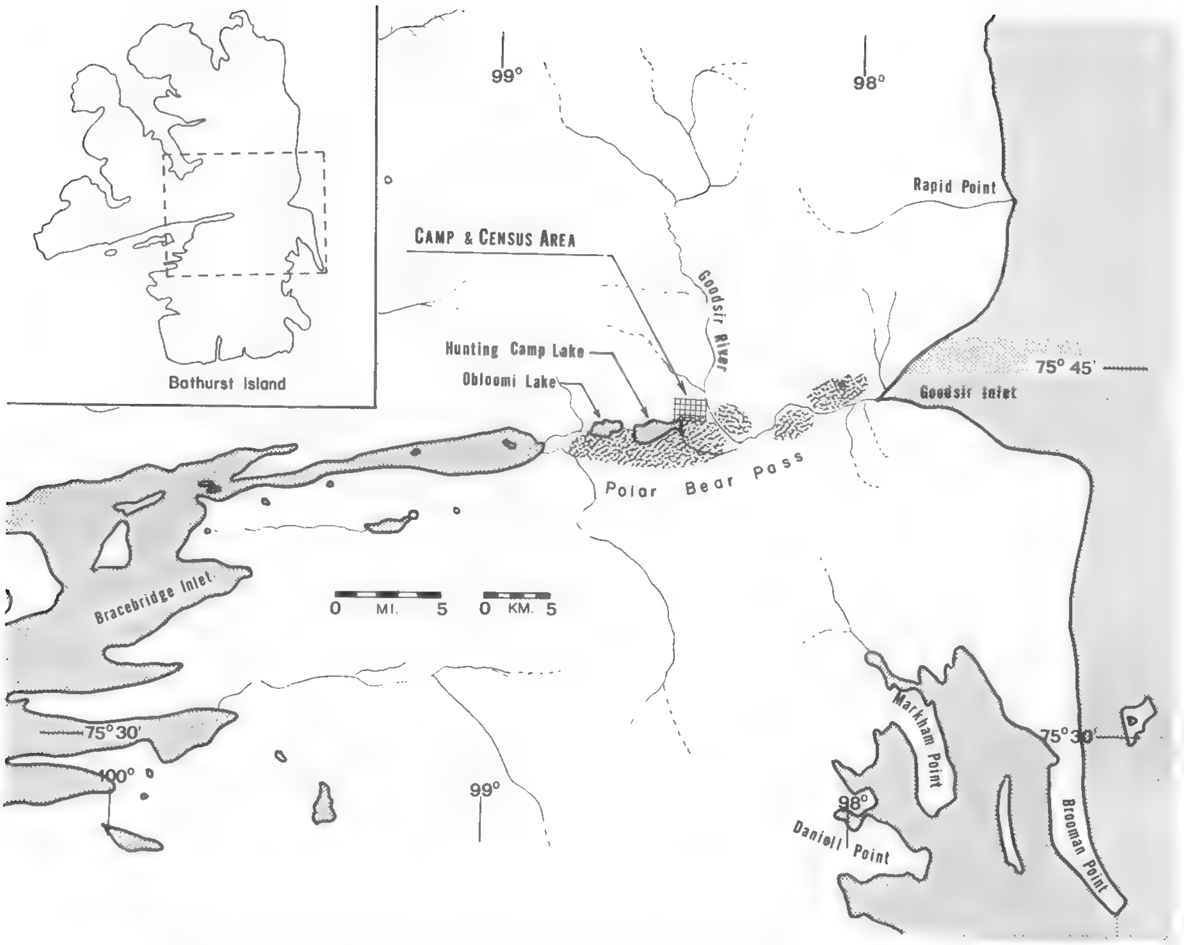

Bathurst Island
99°
98°
Rapid Point
CAMP & CENSUS AREA
Goodsir River
Hunting Camp Lake
Obloomi Lake
75° 45'
Goodsir Inlet
Polar Bear Pass
Bracebridge Inlet
0 MI. 5
0 KM. 5
75°30'
100°
99°
Markham Point
98°
Daniell Point
75°30'
Brooman Point

Figure 3. Central Bathurst Island. Coarse stippling shows sedge-moss wetlands inhabited in summer by Red Phalaropes. Lakes and inlets thaw early in summer from meltwater while the ice is still solid on the sea outside. Inset shows the portion of Bathurst covered by this map.

shorebirds, including phalaropes, paused here before dispersing to other locations, but their numbers were never large enough to warrant the title of a staging area.

Pair Bond

The earliest groups seen each season included both mated pairs and unmated females. I did not have an unequivocal record of an unattached male. Close association of the two birds marked the pair bond. When walking or swimming, resting or feeding, the pair usually stayed close together, sometimes almost touching heads and twittering softly. These prolonged, high-pitched notes are so faint they are audible only at close range, and no other observers have mentioned them.

At first I supposed these pair bonds had been formed before arrival, but later realized the pairs might have been formed almost instantly after the appearance of the male on the nesting ground as in the Spotted Sandpiper, *Actitis macularia* (Oring and Knudson 1972:65). Such quick pairing might suggest a carry-over of attachments from the previous year, but I doubted this in view of the briefness of the pair bond, the readiness of the female to pair immediately with another male, the separate departure of the sexes in fall migration, and the low rate of return to the same nesting sites reported elsewhere. At arrival the males probably are ready to breed, as shown by enlargement of the testes (Kistchinski 1975:294) and as suggested by their plumage and behavior while still many days and 4,000 km short of the nesting ground. At the latitude of San Francisco, some migrating Red Phalaropes are in full breeding (alternate) plumage (Storer 1951:193), and the sexes interact vigorously (Bent 1927:3). Red Phalaropes in Alaska showed a low tendency (7 of 90 males and none of 30 females) to return to the specific tracts used for nesting in previous years (Schamel 1977:320), but Northern Phalaropes in Finland showed "strong site fidelity" and some definitely paired after arrival (Hilden and Vuolanto 1972:62). In Wilson's Phalarope, which reaches its nesting ground well in advance of egg-laying, the most intense competition for mates occurs in the early stages of pair-formation (Howe 1975a:21), which is reduced almost to the vanishing point on Bathurst Island. These circumstances are consistent with quick formation of the pair bond on the nesting area, but they do not completely rule out initiation of the bond prior to arrival.

The pair bond is ephemeral. It ends quickly as the male, occupied at the nest, virtually abandons the female. She can initiate a bond with a different male even before her first clutch of eggs is complete, although in some cases the bonds may persist for a few days beyond egg laying (Schamel and Tracy 1977:316–320). Tinbergen (1935:26) noted renewed signs of sexual behavior in female Northern Phalaropes immediately after the laying of the fourth egg.

Contests for Males

Others have remarked on the noisy conflict among phalaropes, especially Northern Phalaropes, whose females "fight by the hour" according to Brandt (*in* Bent 1927:18). In contrast, I found calm and sociability rather than struggle to characterize Red Phalaropes on Bathurst Island. Perhaps the sparse population, late date of arrival, and quick pair formation tended to minimize conflict.

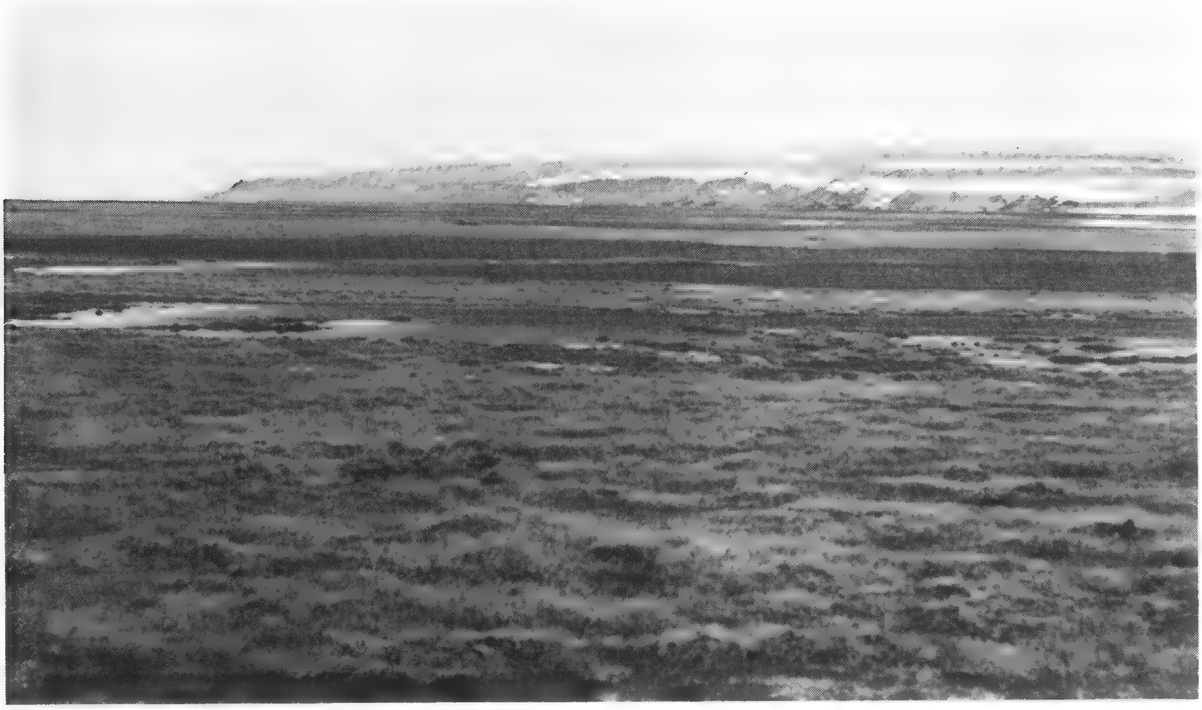


Figure 4. Polar Bear Pass, a wet valley with freshwater ponds and lakes, is feeding and nesting habitat for the Red Phalarope. These birds avoided the dry hills.

Occasionally females challenged established pair bonds. In one instance I witnessed a prolonged encounter from beginning to end. A pair was feeding and idling on grassy land that appeared suitable for nesting. It was still early in the season, 27 June, and their behavior led me to suspect they had not yet started nest-site searching. I was not aware of any other phalaropes within sight, but suddenly four females descended on them. The flashing of wings was so rapid I could not always identify the participants even though I moved up to within three paces of them. The male lay flat on the ground, head and bill extended, eyes closed, while his mate covered him with her body and outspread wings. At times he burrowed under her like a juvenile brooded by a parent. The attacking females jabbed with bills and flailed with wings. At times she leaped or fluttered upward to meet them on even terms. The contest proceeded in flurries broken with rest periods, during which the challengers stood about panting heavily. In lulls, the male revived and sometimes darted at a nearby female or scuttled along the ground to crouch in a frost crack or cleft in the moss. Any activity on his part invariably incited the females to fresh attack. They swirled about me as though I were not there, all the while uttering loud, shrill, rapid cries.

The entire episode lasted 35 minutes, and the group drifted 50 meters in the course of it. After it was over, the bedraggled male spent one-half hour restoring his plumage to normal appearance. His mate stood very close, facing him with outthrust breast. Each time he turned, she moved quickly around to interpose herself in the direction he faced. This was the most extreme form of a posture often assumed by females in the presence of their mates, described as "pushing" by Bengtson (1968:9).

Another time, on 30 June, I heard the sounds of conflict at a feeding area on the edge of a lake. I ran to the spot and saw two females fighting over a male that was being pressed down into the water but was making his way directly to his nest 400 meters away. As in the previous instance, one female hovered or stood over him, and the other darted at her from above. The male, running and fluttering along the ground, progressed about as fast as I could keep pace by trotting. The contest continued until the male was about 20 meters from his nest, when both females flew away. He settled on the eggs immediately. I had found the nest five days previously with a complete set of eggs, and interpreted the defense by the female to indicate the pair bond was still intact. If so, this duration was the longest of any pair bond I noted.

On another occasion I saw a female dart aggressively at a male with her bill outthrust, causing him to take short flights repeatedly to avoid her. Finally, he flew directly to his nest, where he had been incubating a full set of eggs for one or two days. At other times it seemed to me the return of the male to his nest was initiated by a mere gesture of aggressiveness on the part of the accompanying female. Other observers also have noted males early in incubation being "chased back to their nests" by females (Parmelee et al. 1967:138).

Several times I saw brief events that pointed to affirmation and reinforcement of the pair bond through interaction with other individuals. Males darted with outstretched bill toward other females and instantly returned to put their heads up close to those of their own mates. One day three pairs were feeding amicably at close quarters in a small puddle near my blind. Without any provocation I could detect, they exploded into the air with shrill calls. Then, almost as suddenly, they settled back to the place they had left. However, they now stood rigidly for several seconds, each pair head

Figures 5 *(above)* and 6 *(below)*. Habitat of the Red Phalarope on Bathurst Island.

to head, before they resumed feeding as before. I interpreted this flurry to be a startled response to a mistaken challenge. At the time I was concealed, and there were no predators or other disturbances apparent to me.

Auditory Signals

An active and gregarious bird, the Red Phalarope has a wide repertoire of movements, postures, and vocalizations for communication. Yet it does not show many of the conspicuous displays of other sandpipers—upraised-wing postures, elaborate aerial performances, and sustained song. Many of its courtship and agonistic signals are subtle, and I did not achieve sufficient familiarity with them to be confident of their significance. So I mention here only those unmistakable to me, the auditory signals.

Red Phalaropes have no prolonged or elaborate vocal displays, but they communicate with a variety of simple notes and with whirring wings. They made some of these sounds under so many different circumstances I was frequently baffled to understand the purposes of them. The difficulty of describing bird sounds with words is notorious, and I am unable to recognize some notes mentioned by other authors; so I will start afresh with these descriptions:

Location Note

The Red Phalarope has two loud single-syllable calls; one has a vibrating or buzzing quality signified here by the letter Z, and the other is a clear musical note described in the next paragraph. The buzzing *zeeet* call is the most far-carrying and distinctive note of the species. Phalaropes on the wing or on the ground at a distance are readily distinguishable from other shorebirds by this sound. Often it brings a response in kind if another phalarope is nearby. I have heard it from a female flying toward a male on the nest, and I have heard him answer from the nest. Often both members of a pair give it when momentarily separated and out of sight of one another or when about to fly. The note is slightly more prolonged than a simple, explosive chirp, as indicated by the *eee*, but it still lasts only a fraction of a second. A person can hear it almost a kilometer away on a quiet day.

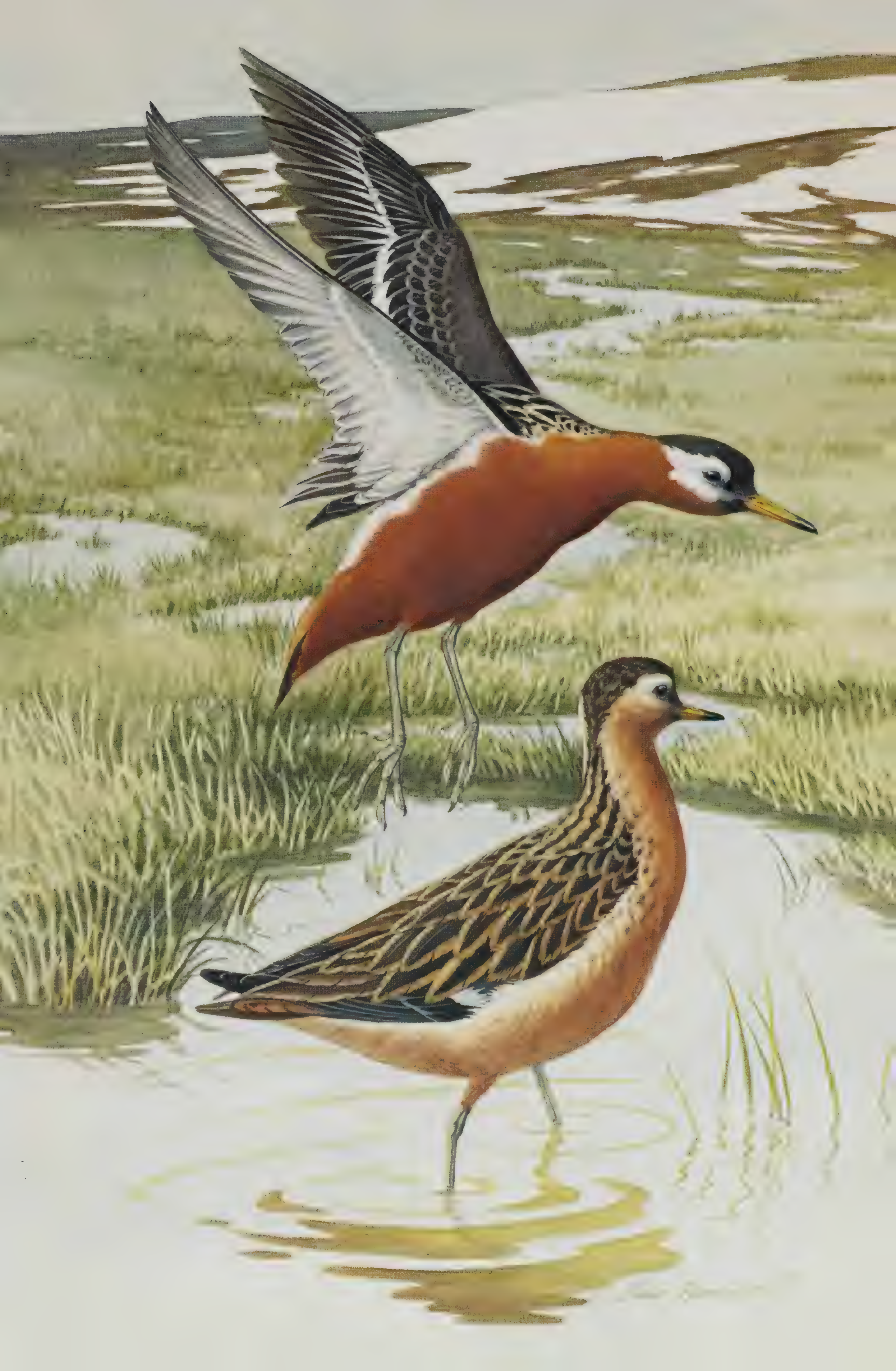
Excitement Signal

This loud, clear, musical note *(peep)* lacks any of the buzzy quality of the previous call. I suspect the intensity of it, as well as the tonal quality, can convey alarm. When several females were fighting near a male, they filled the air with this call, indicating not fear but a high level of excitement. When a male with a brood uttered it, the young crouched without moving. When a male uttered it near a female shaping a nest cavity, she stopped work and raised her head alertly. In both cases of alarm the stimulus was a flying jaeger some distance away.

Intense "Irritation"

Occasionally when male phalaropes were flushed off the nest, they uttered low-volume, harsh, rasping calls *(rrrrt)*. I have also heard this sound near downy chicks away from the nest when the male was at hand to brood them but was prevented by my presence. If a male displayed at the nest when frightened from it, this was one of his sounds.

Red Phalarope, *Phalaropus fulicarius*. Painting by Diane Pierce.



Socializing Twitter

Phalaropes uttered a soft, rapid series of faint *ti-ti-ti-ti* peeps almost continuously when the male and female of a pair were associating while feeding, nest building, or loafing. It was one of the signs of the pair relationship. It invariably occurred before and during copulation. It could be heard only if the observer was very near.

Rallying Call for the Brood

This unmusical double noted *wee-cha* or *choo-eet* was repeated steadily by the male when in company with a brood of chicks. It was low in volume and pitch, and slightly rasping in quality. In one male the call *wee'-cha* was accented on the first syllable and then dropped in pitch and volume on the second; in another male it was accented and rose in pitch and volume on the second syllable, *choo-eet'*. But each male was consistent with his own pattern, and doubtless the young were imprinted to his distinctive sound.

Miscellaneous Calls

In addition to the foregoing calls whose function seemed clear, I detected other notes that I could not categorize. Several times I heard double notes that sounded like *tweedle*, and at other times I heard clucks that reminded me of chickens in a barnyard. The recently hatched young have very high-pitched, faintly audible peepings much like the downy young of many birds.

Calls of Other Phalaropes

The calling of Northern and Wilson's Phalaropes seems generally similar to the Red, but some notes are different if we can judge from the word descriptions. Observers of Wilson's Phalarope, particularly, describe a harsh grunt more like a sound of certain sandpipers than the Red Phalarope.

Wing-whirr

Everyone who has studied the Red and Northern Phalaropes has commented on their distinctive manner of hovering momentarily with noisy flapping of wings. Usually the bird springs up from the water or ground and hovers a second or so, wings beating vigorously, feet drooping, and head stretched forward and held low. Sometimes the bird merely stretches upward and flaps without leaving the surface. Afterward it usually flies away but sometimes it settles back and resumes its former activity. Both sexes perform it, but the female more often.

The rapid wing movement and its sound reminded me of a miniature helicopter, and with Höhn (1971:344), I consider "wing-whirr" more descriptive than "rattling" used by some other authors.

Tinbergen (1935:520) took it as a sign of sexual readiness and invitation — a prelude to copulation on the part of both sexes in the Northern Phalarope. Bengtson (1968:7) believed it "invites the male" and "occurs in sequences of courtship displays preceding copulation." Both men had experience with a very small number of birds. Although, in my experience, the wing-whirr occurred at such times, it also occurred many times in situations unrelated to sexual activity. I saw both members of a pair perform it just before copulation; the female alone, just before copulation; the female, just after copulation. But more often I saw it occur without apparent cause or consequence: a male as he left a nest, a lone female with no other phalarope near, a female in a group of feeding females, and a female flying away from the company of a male. Often, it seemed to me, the wing-whirr occurred after a period of inactivity. I did not judge that it correlated closely or necessarily with the copulatory act, although sometimes it was incorporated into the sequence of acts at the moment. This association could be incidental.

Höhn (1971:344) suggests there may be two kinds of wing-whirr, "simple wing whirring," which occurs at the start of a flight, and "wing whirring with hovering," which is precopulatory display. I was not aware of just two distinct forms, but noted a wide range of intensity.

To me, the wing-whirr seemed a manifestation of tension. It was at its height in the breeding season and burst forth at intervals almost like song in passerines. It served as an announcement of the individual's presence and also as a species recognition signal, catching the eye as well as the ear.

It is tempting to speculate if this distinctive gesture of the breeding season is derived from some movement useful to the bird at other seasons. It may be an elaboration of wing-beating used in a stormy sea to free the plumage of spray and foam. Also, a helicopter-style takeoff may be suited to a turbulent sea, and at the same time it may provide a visual signal to other members of the species. It seems significant that this behavior occurs only in the Red and Northern Phalaropes, the sea-going species, and not in their relative, the Wilson's Phalarope, which spends its life in the sheltered waters of the interior. Höhn (1971:344) says it occurs only in breeding season, but since these birds have been observed mainly in distant and fleeting glimpses at sea, I wonder if a closely related movement, perhaps less intense, has passed unnoticed at other times of the year.

Although the full expression of the wing-whirr does not occur in the Wilson's Phalarope, Howe (1972:123) noted a silent "hovering," which he interpreted as a comfort movement sometimes preceding copulation.

Polygamy

The emancipation of females from nesting duties among phalaropes has been known, and the presumption of polyandry has existed for a long time; but the evidence has been slow to come. Polyandry is a rare circumstance among birds, reported in less than one percent of the species studied (Jenni 1974:131).

The likelihood that the female might lay more than one clutch in a season with the same or different mates is suggested by several circumstances: the short pair bond, the spread of nest-starts over a period of nearly four weeks, the low weight of the egg compared to the weight of the female, and the ability of the female to produce successive eggs in less than 24 hours.

In 1970 I suspected three females laid second clutches with different mates on the study area I was watching intensively. A cluster of nests was completed between 1 and 5 July at the corners of a triangle 70 × 120 × 135 meters. While these males incubated, a second cluster of nests cropped up 200 meters away, placed similarly 75, 125, and 130 meters apart. Here the sets of eggs appeared betweeen 9 and 12 July; that is, 4 to 11 days after completion of the first clutches. I saw only three females frequenting this section of the marsh, but since the birds were not distinguishable, I could not be sure there was only one trio.

In 1973 I preserved the ovaries of two females and brought them back to Robert B. Payne for microscopic examination. Post-ovulatory scars showed that one of the birds had laid two clutches of four eggs in rapid succession, and the other bird was about to lay its first set. It was uncertain whether multiple laying had provided a replacement clutch for the same mate or eggs for a second mate.

Proof of polyandry is now available for both the Red and Northern Phalaropes. At Barrow, Alaska, Schamel and Tracy (1977:316–319) found four banded females laying two clutches of eggs at three- to five-day intervals with different mates. Among Northern Phalaropes in Finland, Raner (1972) first reported polyandry, and Hilden and Vuolanto (1972:69–72) concluded it was a normal occurrence when there was an excess of males present.

A particularly interesting parallel with the phalarope occurs in the Dotterel, *Eudromias morinellus*, in which the female is larger, more brightly colored, and emancipated from the care of eggs and young; here also monogamy is usual but polyandry occurs when there is a local excess of males (Nethersole-Thompson 1973:50). Serial polyandry also is known to occur in at least three species of arctic sandpipers (Pitelka, Holmes, and MacLean, 1974).

The origin and adaptive significance of female emancipation and polyandry in phalaropes has not yet been fully explained. However, the ecological conditions for predicting polyandry according to Emlen and Oring (1977) were neatly fulfilled in this population of Red Phalaropes. The breeding conditions were subject to extreme fluctuations, with food supply varying from abundant at one time to precarious at another, and with predation severe in one year and negligible in another (Mayfield 1978).

Although food in the short arctic summer is usually abundant, as judged by the small proportion of time spent by birds in feeding and by the clouds of insects on the wing in warm calm periods, cold weather with snow may occur at any time in the nesting season, severely reducing food resources. These episodes can delay nesting or disrupt it completely. The early departure of females while the males are incubating reduces the pressure on the food supply by almost half, and the subsequent departure of the males after a very brief period of attention to the young again makes more food available for the juveniles during the waning summer when shortages are most likely to occur. The special food requirements of Red Phalaropes—mainly diptera larvae and adults—and the restricted areas used for feeding may cause these food supplies to be particularly vulnerable to bad weather. For example, a group studied by Höhn 1971:345) had only two acres of "phalarope marsh" on a small island.

Here we find intriguing parallels with the Pectoral Sandpiper, *Calidris melanotos*, in Alaska. In that species the pair bond is short, and the male, the larger member, departs before most eggs are hatched. The food, as with the Red Phalarope, consists mainly of the larvae of dipterous insects which decline in abundance in mid-summer (Pitelka).

The emancipation of the female phalarope makes it possible for her to produce successive clutches quickly with full time to build her nutritional resources and without delay caused by intervening physiological changes for incubation. The possible advantages of such a system are discussed by Jenni

(1974) and, with special reference to the Mountain Plover, *Charadrius montanus*, by Graul (1973:87).

Similarly, the circumstances of the Red Phalarope already detailed, particularly the early departure of some females, open the possibility for males whose nests are lost early in the season to replace these with different mates. Indeed, Hilden and Vuolanto (1972:69–72) have found serial polygyny among Northern Phalaropes.

If there is a single word to characterize the mating system of Red Phalaropes, it is opportunistic. The most frequent pattern is a single nesting attempt in a season by a pair (monogamy); under certain circumstances females may provide clutches for two or more males in a season (serial polyandry); and occasionally males may get replacement clutches from different females (serial polygyny); and interspersed among these events are seasons in which hardly any Red Phalaropes nest. This opportunism is demonstrated also by the readiness of the species to exploit locations that are only occasionally suitable and small in extent.

If the geographic distribution of small groups is random, an uneven ratio between the sexes locally is likely to be significantly large. Red Phalaropes often nest in small disjunct populations on small islands or in isolated marshes. Localities in Canada have held as few as two nests (Stewart D. MacDonald, pers. commun.) and "six pairs" (Höhn 1971:336). In Spitsbergen, one place held two "pairs" and another four to five "pairs" (Bengtson 1968:2), and generally the species nested in "small colonies, the biggest consisting of 25 pairs" (Løvenskiold 1964:207).

The Arctic, a geologically recent land, has provided a crucible for rapid experiment in natural selection, and an amazing diversity of breeding strategies have evolved among closely related birds (Pitelka, Holmes, and MacLean 1974).

In recent years a number of arctic shorebirds have shown the capacity to lay two or more clutches in a season with the same or different mates. The Sanderling (Parmelee 1970:97–146, and Parmelee and Payne 1973) the Temminck's Stint, *C. temminckii* (Hilden 1965:1–5) and possibly the Little Stint, *C. minuta* (Kistchinsky and Flint 1973:56–57) lay one set of eggs to be incubated by the male and another set to be incubated by the female. In the temperate zone this pattern occurs among Mountain Plovers in Colorado (Graul 1975:7). Polyandry is a common practice in the Spotted Sandpiper in temperate United States, with females mating sometimes with more than two males, each clutch incubated by a male except the last, in which she shares incubation (Hays 1972:43–57; Oring and Knudson 1972:59–73).

The Nest

Searching for a Site

In establishing the nest, the female participates actively in site selection, to a minor extent in cavity shaping, and not at all in nest lining.

Searching for sites and preparing the nest together probably reinforces the pair bond. It may serve also to space nests a suitable distance apart, as the pairs I watched always withdrew from others and conducted their search with no other phalaropes nearby. Since I did not see two pairs searching the same plot of ground at the same time, I suspected that nests found unusually close to one another may have been established at different times. The searching ritual may also aid in the precise timing of the female's ovulation, as watching the nest-building process is believed to do in the Brown-headed Cowbird, *Molothrus ater*, which builds no nest of its own (Hann 1937:207). I did not see any copulation before this stage.

I followed eight pairs during one or more bouts of searching. Three of these continued for 70 to 90 minutes after I found them under way. One pair traveled 400 meters in this time, but usually pairs meandered about in areas less than 200 meters in diameter. They walked an irregular course, often stooping out of sight between clumps of vegetation. They explored independently but usually within 10 meters of one another, twittering softly. When one paused, pressing and rotating its body as though shaping a nest, the other often came running to the site. They often took turns pressing and turning in the space before moving on and repeating the maneuver elsewhere. This process involved dozens of scrapes, most of which left no perceptible mark but some of which were as fully shaped as the site eventually receiving the eggs.

Nest Building

The phalarope shaped the cavity with its breast, head low and tail raised almost vertically, torso rotating as though screwing the long axis of the body into the ground. This action was signalled by the dark tips of wing and tail visible above the vegetation. In discussing the scrape ceremony of Wilson's Phalarope, Howe (1975b:252) pointed out that a similar ritual is almost universal among members of the order Charadriiformes.

The period of searching and shaping continued as long as four days in one instance, but I believe it may have covered as little as one or two days in other instances, where I did not see it at all but found the clutch started within two days after first noting the pair in the vicinity.

Usually the grass was sufficiently thin, or the birds chose natural spaces between the stems, so that body pressure parted the leaves down to moist soil. Hense a "scrape" was recognizable not so much from its bare floor as from the cavity formed by the surrounding vegetation. Only occasionally did I see a male pluck at standing plants in the cup, a prominent action of the Wilson's Phalarope (Howe 1975b:253), which may have greater need to clear the floor in the more heavily vegetated regions where it nests. The use of the bill is variable among shorebirds, some "scraping" entirely with the body (Lind 1961:70), as in the Red Phalarope.

The male gathered material for the floor mainly from the ground outside the nest itself, and he pressed it into the cavity by rotation of his breast. He did not walk or fly with it. He reached forward, picked up strands, and pitched them backward along his flanks with rapid, machine-like motions. His movements were so quick and the particles often so small I could not always be sure any material was being transported. As the male flicked his bill with such casual aim, the fragments scattered and many were snatched away completely by the wind. Since loose material on the brink of the cavity was scarce, this method served to transport leaves toward the nest by stages and at the same time avoided conspicuously denuding the ground immediately about the nest. Similar "sideways throwing" takes place among shorebirds, gulls, and terns as well as among more remote families of ground-nesting birds (Harrison 1967).

In one instance a pair alternated in a cavity for 15 minutes, she sitting steadily for one five-minute period and he pitching grass steadily for two three-minute periods. At the end of this time I could not detect any more lining than might have been deposited by the wind. Then the pair did not use this site but chose another 60 meters away, where the female laid her first egg three days later.

The lining of the nest was slight or invisible when the first egg was laid but continued to grow as eggs were deposited and even after the clutch was complete. For example, in one instance the first egg was laid on bare dirt with very scanty grass around it. In the six-hour period before the arrival of the second egg the male worked steadily for periods of 55 and 65 minutes, ranging outward as far as 50 cm. By this time a thin layer of straw covered the floor. This lining continued to grow thicker throughout the egg-laying period. Once I saw a male throwing vegetation desultorily at a scrape 60 meters from his nest, which contained one egg at the time.

Nest Materials

The nest floor consisted of whatever fine substance lay loose nearby. In one nest the lowest layer was grass and the upper layer was willow leaves, but this arrangement may have resulted from the bird's gathering material farther away in the later stages of flooring. Sometimes the flooring was little more than a few strands, but two well-lined nests dried five days under room conditions weighed as follows: all grass or sedge, 4.3 grams; mostly willow leaves, 5.1 grams. In other regions nest flooring may include a variety of other materials, for example, in Spitsbergen, small flattish stones, lichens, stems of saxifrage, feathers, fox hairs, and occasionally nothing at all (Løvenskiold 1964:209).

Nest Location

Usually the nest (Figure 7) was placed in sedges tall enough to cover it completely, but sometimes the vegetation was so thin that mere wisps drooped over it. Such scanty cover did not completely conceal the eggs but cast obscuring strips of light and shadow over them. Elsewhere the species has been known to nest in places with virtually no vegetation. Perhaps suitable food in abundance is an attraction overriding the usual nest-site preferences.

On Seymour Island, a bare islet 30 km north of Bathurst Island, Stewart D. MacDonald (letter dated October 1975) found two nests. One was placed on the rim of a former nest built of moss by an Ivory Gull, *Pagophila eburnea*, and the other was placed on a mat of purple saxifrage with tendrils pulled from an adjacent rock to make a canopy. Løvenskiold (1964:209) mentions open nests on piles of seaweed in Spitsbergen.

I found no nests over standing or trickling water, but sometimes there was water at the threshold. Nests surrounded by water when built often had none a few days later as the thaw progressed. Occasionally a rise in water may flood a nest and cause it to be abandoned. David F. Parmelee and Philip Taylor (letter dated 10 April 1972) found a nest 2 July 1968 with two eggs partially submerged in water. The next day the nest received an additional egg but then was deserted. In Alaska, Brandt (1943:397) found some nests over shallow water, and he noted that nesting material added by the birds lifted the floor to a dry level.

Figure 7. Harold Mayfield pointing to Red Phalarope nest site concealed in sedges and grasses. Photograph by Ralph Palmer.

In the placement of nests I could not detect any consistent relationship to landscape features — ponds, marsh edge, beach ridges, frost mounds, or boulders — except that nests were always in moist portions of flats.

Although freshwater pools were a prominent feature of the nesting habitat, I could discern no more tendency to nest near ponds than chance would dictate in this terrain. On my census area in 1971, I paced the distances of 15 nests from the nearest pond, recording a range of 5 to 200 meters with a mean of 67 meters. Here, it would be hard to find a spot more than 200 meters from a pond without leaving the sedge-moss habitat entirely. In another tract where ponds were very close together, one nest was placed six cm from a small pool and another was less than one meter from a larger pond, but here the nesting sites were compressed to narrow isthmuses.

It seemed to me that phalaropes, like human beings, spread out their homesites but still chose locations not far from neighbors. Nests were scattered, not at random, but in clusters. Each group usually held three to five nests spaced less than 200 meters apart, while considerably more distance than this intervened between the "colonies." The nests in a cluster were close enough for a bird at one to be easily aware of voices and movements at others. My principal study area lay in a fairly uniform expanse of wet flats extending for more than two km along the foot of a ridge, but the nests were bunched each year in portions of those flats, leaving empty areas that looked equally suitable. It is possible that the gradual retreat of snow and water promoted clustering, allowing different parts of the flats to become attractive for feeding and nesting at different times.

I had no nests closer than 35 meters, but Parmelee et al. (1967:137) found nests as close as six meters on Victoria Island where the available habitat was compressed into narrow strips. On Jenny Lind Island he found two nests only three meters apart (letter dated 10 April 1972). In northeastern Siberia, Kistchinski (1975:297) found nests three and six meters apart.

Others have noted clustering of nests of Red Phalaropes. Kozlova (1961:8) and Løvenskiold (1964:207) refer to "colonies" but did not speculate if these were a consequence of restricted habitat or social attraction. Höhn (1965:46) remarked that all three species of phalaropes nest " ... mostly in loose colonies of four to eight pairs; solitary pairs are rarer."

Clustering of nests, provided they are not so close that destruction of one exposes another to discovery, probably confers an advantage through group warning and defense.

It is apparent several factors may influence choice of nest location, and the only universal requirements is an abundance of suitable food.

Absence of Territoriality

I saw no male or female defend a territory around the nest or at the feeding and loitering areas. Incubating males showed wariness but not aggressiveness at the nest. Once I watched a male feed within two meters of an incubating male without visible response. Another time I herded a walking male toward a neighboring nest, and he stepped almost over the head of the male sitting there without noticeble reaction from either. Even the female's defense of her mate seemed a defense of position or posture with respect to him rather than simply a defense of space, for at times a female, while feeding, almost touched a male in the presence of his mate without challenge.

Absence of territoriality allowed members of this species to share rich feeding areas and extremely restricted nesting zones.

Copulation

Copulation (Figure 8) occurs just before and during the egg-laying period. I saw copulation during nest-site searching more than a day before the first egg, but the only instances I could time fairly closely with respect to egg deposit were as follows: 12, 7, 6, 6, and 4 hours before the first egg; 5 and 6 hours after the first egg; 4 and 2 hours before the second egg; one-quarter hour after the second egg; 2 hours before the third egg; one-quarter and 5 hours after the third egg.

During copulation the male crouched on the back of the female, holding his position with fluttering wings. He held his bill straight forward parallel to hers, not touching the feathers of her head. Nearly always the act occurred on land or in water shallow enough for wading, but twice I saw it in water of swimming depth, the female almost submerging under the weight of the male.

Seven mountings (timed by counting) required 6, 7, 8, 8, 8, 8, and 10 seconds. The duration, while longer than for many species of birds, was much shorter than for Wilson's Phalarope, which averaged 27 seconds (Marshall Howe, pers. commun.). Here, as in other respects, Wilson's Phalarope behaved more like the sandpipers, in some of which the act is much more prolonged — for example, the Sanderling, which usually requires more than 40 seconds and occasionally two to three minutes (Parmelee 1970:113).

The only unambiguous invitation by the female was a slight crouch with the bill held level or slightly lifted, as distinct from the resting angle which has a slight downward tilt. The male did not always respond, but I believe the crouch is the usual prelude to successful copulation. In three instances when I was sure it did not occur, males mounted females briefly but coition did not take place. Many times I was not aware of any invitation, but there may have been cues too subtle for me to notice. During copulation a twittering was barely audible, and sometimes I heard it beforehand, leading me to suspect there may be vocal preliminaries also. Other actions by the female occasionally preceded the crouch; for example, twice females brought the males to them by rotating in the nest-scrape posture, and many times the wing-whirr drew my attention, but this signal came so frequently I did not associate it especially with copulation.

One unusual movement of males appeared appetitive. A few times I saw males spring up and down rapidly, 20 cm high, as though bouncing in front of the female, but in each instance she gave no response and copulation did not ensue.

The behavior of the pair after copulation was variable. Often the male walked or flew away with the female following closely, but this was not the invariable pattern. Sometimes they both resumed feeding where they were, or one of them departed alone. I saw copulation repeated within five minutes, but usually the interval was 30 minutes or more.

Copulatory behavior is more elaborate and ritualized in the Wilson's

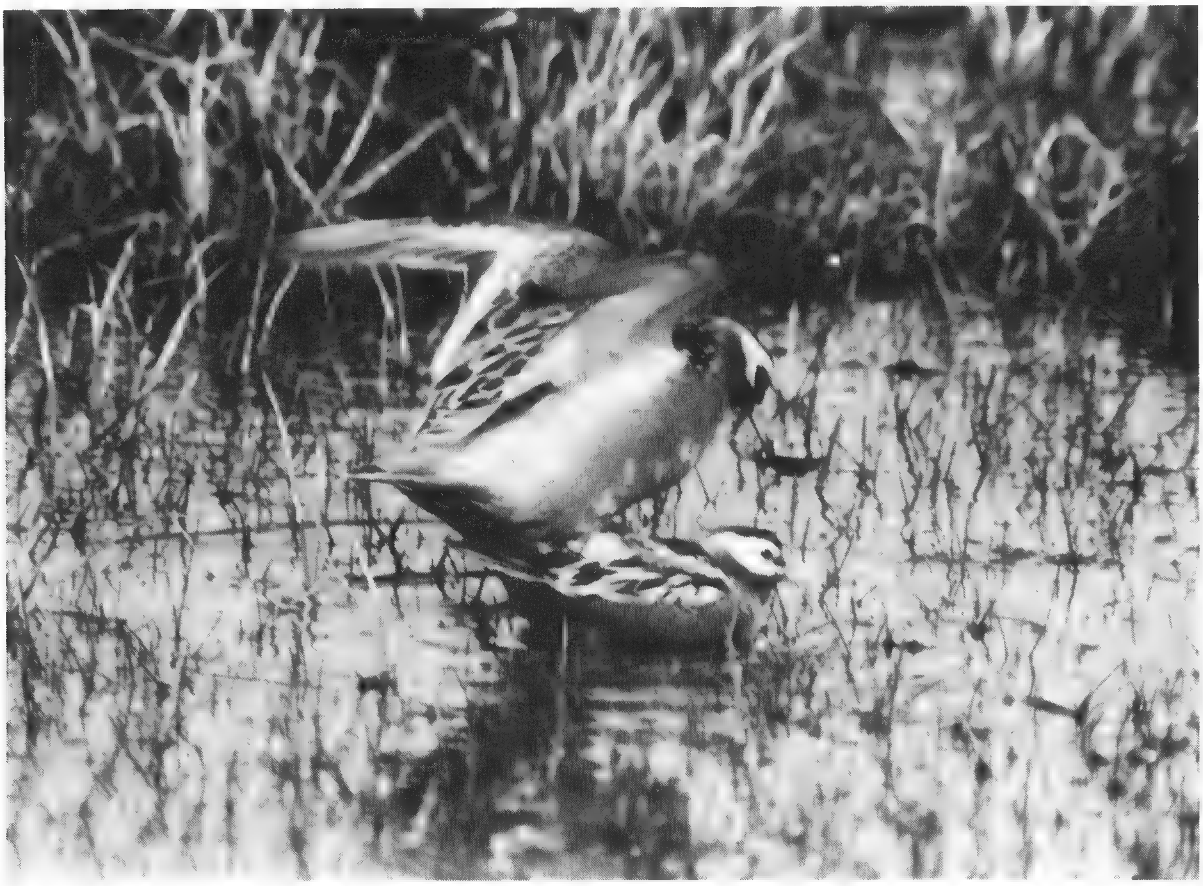


Figure 8. Copulation usually takes place just before and during the period of egg-laying.

TABLE 1

Intervals Between Eggs Laid

Nest number	*Hours between laying of*			*Date of first egg*
	Eggs 1 and 2	*Eggs 2 and 3*	*Eggs 3 and 4*	
12	—	34*	22	21 June 1971
14	24	22	22	9 July 1971
15	—	22	23	28 June 1971
16	—	22	—	29 June 1971
18	—	26	—	2 July 1971
32	28	24	22	30 June 1973
33	24	26	22	30 June 1973
34	25	24	—	6 July 1973
36	—	22	21	7 July 1973
Mean	25.2	23.5	22	

*Exceptionally long interval omitted from calculation of mean. This egg came earlier in the season and during colder weather than the others.

than in the Red Phalarope, according to studies of the former species (Höhn 1967:229–231, and Howe 1975b:254–257).

Eggs and Egg-laying

The time separating early and late nests was more than enough to permit second clutches by some females. In three years, the observed spread from the start of the first clutch to the start of the last clutch found was as follows: 17 days in 1970, 26 June to 12 July; 23 days in 1971, 18 June to 11 July; and 18 days in 1973, 20 June to 8 July. The true span may have been greater than that observed, because I may not have found the very first and last nests of the year. On Victoria Island, where the summer is a little milder and longer, Parmelee et al. (1967:139–141) found a spread of more than a month in the ages of young, and at Hooper Bay, western Alaska, Brandt (1943:396) likewise found "the period for fresh eggs spread out over one month."

I was able to determine the intervals between the laying of eggs in 19 instances (Table 1). The sample was small, but it appeared the intervals became shorter and more uniform as the clutch progressed, becoming less than 24 hours before the last egg in every instance.

In this region of continuous daylight during the nesting season, the time of egg deposit was not limited to any part of the day. For 35 eggs I was able to place the laying time within one-half day; 24 (69%) were laid after noon, and 11 (31%) before noon. In four known instances, and perhaps others, eggs were laid in the middle of the night, between 22:00 and 02:00.

Among 62 clutches examined by me or my associates on Bathurst Island, 55 (89%) had 4 eggs, 6 (10%) had 3 eggs, and 1 had 5 eggs. This distribution is generally consistent with samples from other regions, except that two-egg clutches are reported regularly (Kistchinski 1975:299, and Douglas Schamel, unpubl. data). Clutches of five eggs and larger are exceptional among phalaropes but not unprecedented, i.e., six eggs for the Red Phalarope in Spitsbergen (Løvenskiold 1964:209), and 5, 7, and 8 eggs in the Northern

Phalarope (Bent 1927:19, and Congreve and Freme 1930:223). In such instances others have suspected two females may have been involved. I had no evidence bearing on this question. My five-egg set was destroyed by a predator before hatching.

On five occasions (2 nests) I watched from a blind as females entered nests to lay eggs. The periods on the nest were as follows: second egg, 11 and 18 minutes, with departure 4 and 3 minutes after deposit; third egg, 14 and 15 minutes, with departures 5 minutes after deposit in both cases; fourth egg, 13 minutes, with departure 6 minutes after deposit. At the moment I believed to be the time of deposit, she raised her body slightly, throbbing rhythmically, her tail lifted and her head low. Once just after the egg was laid, both the male and female put their heads into the nest together, an action noted in the Northern Phalarope by Tinbergen (1935:12).

One male remained within 10 cm of his mate during two egg-laying episodes, and another male was in sight only once during three episodes, sleeping 10 meters away. Several times I came upon females while laying eggs. In about half of these the male was close by, sometimes crouched or moving restlessly, dabbing with his bill at the ground or at his feathers. In other instances I did not see the male; however, this ratio is not precise because I usually retreated immediately to avoid disturbing the birds. The male of the Dotterel also remains close to the female while she is laying eggs, and he ultimately takes over the nest for incubation (Nethersole-Thompson 1973:69).

Red Phalarope eggs are smaller with respect to body size than those of several other arctic shorebirds known to lay multiple clutches. Red Phalarope eggs according to Schönwetter (1960:418) have a mean weight of 7.5 grams, females a mean weight of 45 grams, and therefore eggs weighing 16.6 percent of body weight. These weights were distinctly less than those of Uspenski et al. (1962:78) reporting four eggs with mean weight of 10.2 grams, and nine females examined in Arctic Canada by Parmelee and me showing a mean weight of 61.7 grams (none as small as 45 grams), but yielding a similar ratio of less than 17 percent. This is below the ratio for the Sanderling (18.7%), Dunlin, *Calidris alpina* (21.4%), Temminck's Stint (19.3%), and Little Stint (21.0%) reported by Schönwetter (1960–1966). The Spotted Sandpiper nesting in a temperate zone produces as many as four clutches in a season (Hays 1973:54), and lays an egg weighing 19.0 grams (Schönwetter 1963:409), which is 19 percent of the mean weight, 46.7 grams for 10 breeding-season females recorded on specimen labels in the University of Michigan Museum of Zoology.

Incubation

The male began sitting briefly on the first egg and for increasingly longer periods as the clutch grew (Figure 8). But he probably did not bring the eggs up to the requisite temperature for development until the clutch was almost complete, for all the eggs hatched within a 12-hour period. Nevertheless, his sitting on the eggs may have protected them from freezing and also from the view of predators. On the first egg, males sat no longer than about 10 minutes at a time. On two eggs, the attentive periods went up to 30 minutes, but these were restless times, the male fidgeting, rising, and moving about to add vegetation or arrange it over the nest. A nest with one egg remained unattended more than three hours, but with two eggs the longest unattended period was 40 minutes. After the third egg, the male appeared to be incubating normally.

I watched four nests for a total of 10 hours when two to eight days into incubation. The males' attentive periods ranged from 33 to 70 minutes, and absences 7 to 12 minutes. The usual absence was about 10 minutes if the male left voluntarily, but only one or two minutes if I chased him off. The incubating male sat low under his bower. Occasionally he arranged the strands over his head, lifting individual blades with his mandibles and pulling them over him from both sides in such an orderly way that they appeared combed. The result sometimes resembled a tunnel with entrances at both ends.

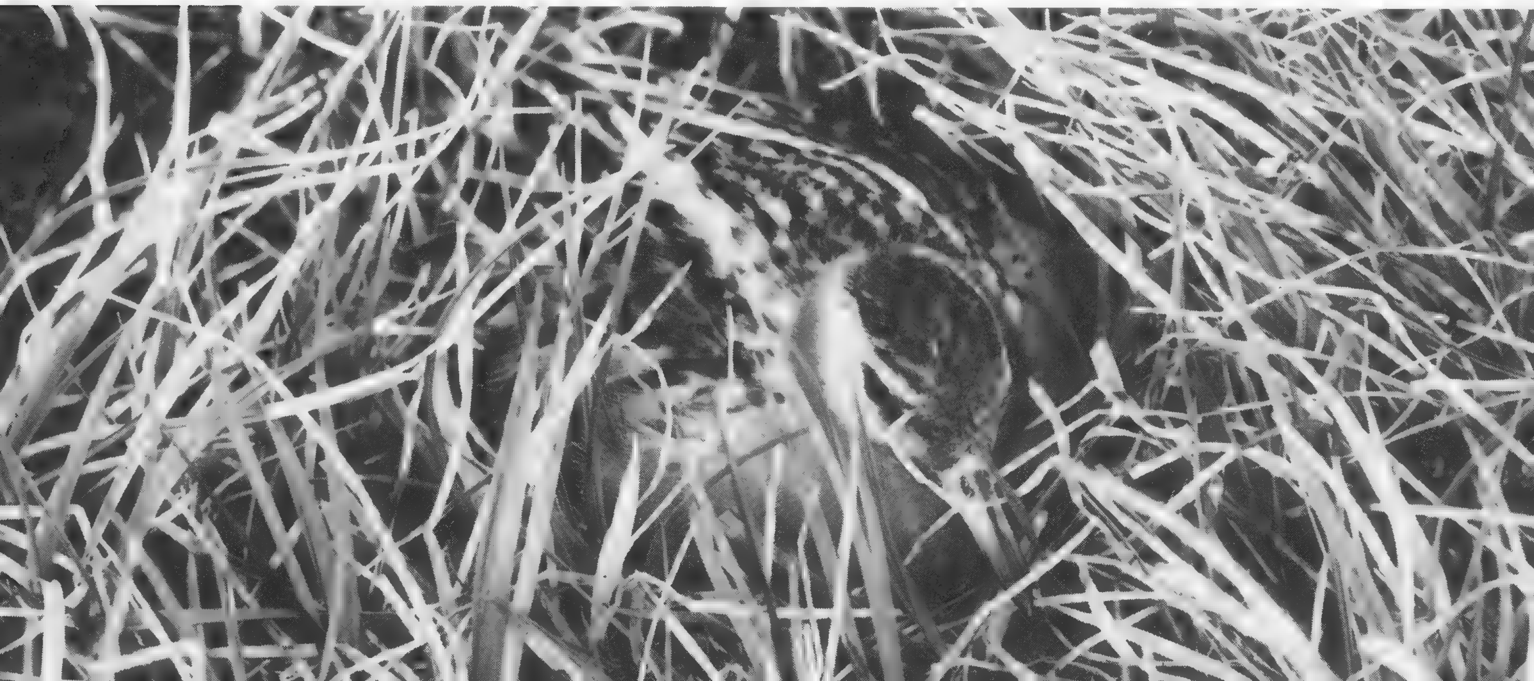
When approaching the nest, the male usually walked the last 10 to 30 meters in a zigzag path between hummocks, his head held low. When leaving, he stepped out and quickly flew away, or took flight directly from the cavity.

Incubating males differed greatly from one another in their reactions to danger. This may account for various reports of other authors, some calling it a close sitter and others saying it took flight when the human intruder was some distance away. I found some males flushed from the nest at 20 to 30 paces, although three to five paces was more common. One individual, during the egg-laying period, allowed me repeatedly to lift it on my index finger to count the eggs, promptly going to sleep after I lowered it back to the nest.

When frightened away, the male ordinarily flew immediately out of sight, but occasionally one circled briefly overhead, calling the clear alarm note. Distraction displays on the ground near the nest were not usual, but a few individuals performed them regularly. Three incubating birds were notable in this respect. One ran from the nest and then crouched two to three meters away with wings half-spread and quivering, all the while uttering soft peeping notes. Another ran from the nest with outspread wings, uttering both clear and rasping calls. A third fluttered away, squeaking shrilly.

Manniche (1910:155–156) in northeast Greenland reported a distraction display in the Red Phalarope, but Parmelee (1967:138), after long familiarity

Figure 9. The male Red Phalarope on the nest forms a bower over himself by drawing the vegetation over his body from both sides. Photograph by Ralph Palmer.



with this species, remarked on the absence of display, in contrast with the elaborate gestures of most arctic shorebirds when frightened from the nest.

I saw no aggressive behavior toward other species at the nest. Phalaropes ignored lemmings running past the entrance. When a White-rumped Sandpiper walked within 15 cm of a sitting male, the sandpiper raised its near wing high in display and hurried on, but the phalarope did not stir.

The main defense of the Red Phalarope was concealment. On the nest or walking through the grass, adults and young reacted first to danger by crouching. However, when a jaeger, gull, or owl flew over a nesting area, phalaropes often flew at them, calling shrilly. The style of attack was distinctive. With its greater speed, the phalarope came up behind the larger bird and crossed sharply in front of it. Apparently this maneuver, repeated again and again, had some success in diverting the predator's attention from the ground, for it turned its head alertly to look above and behind. The phalaropes never touched the bird they were harassing.

I believe the normal incubation period, defined as the period from the laying of the last egg to the hatching of the last egg, of the Red Phalarope is 18 to 19 days, although some clutches, particularly those early in the season and subject to chilling, may require extra time. In one nest the incubation period was 18 days, 1 (±1) hour, the last egg hatching at 21:50 on 13 July. In two instances I was uncertain of the duration because one or more eggs did not hatch: 18 days, 16 (±2) hours with two eggs not hatching, and 19 days, 18 hours with one egg not hatching.

These incubation periods were similar to those determined by Parmelee et al. (1967:138, 225) on Victoria Island—18 days, 17 (±14) hours—and on Jenny Lind Island—17 days, 17 (±5½) hours, and 17 days, 9 (±3½) hours. Brandt (1943:397) reported 18 days, and Douglas Schamel (pers. commun.) also in Alaska found one at 18 days, two at 20 days, and one at 21 days. Pederson (*in* Salomonsen 1950:259) gave 23 to 24 days. With the Northern Phalarope in Finland, Hilden and Vuolanto (197:75) found incubation periods among 26 clutches to range from 16.8 to 20.7 days, three-fourths falling between 17 and 17.5 days.

Hatching

Twice I watched nests at length during the hatching period. At this time the male sat very closely, remaining on the nest as long as 100 minutes and returning within five minutes. While on the nest, he continued to behave much as he had done during incubation, often dozing with eyes closed, and still continuing to arrange the grass over his head.

As the young broke from the egg, he carried away loose pieces of shell promptly, flying in a different direction each time. He disposed of the fragments 20 to 150 meters from the nest and returned almost instantly. In two instances I saw the shells fall in flight, perhaps snatched from his bill by the wind, and he made no effort to retrieve them. Whether the male ever eats the shell I was not able to determine because the birds were not clearly in my sight when they disposed of the shells. Palmer (Grinnell and Palmer 1941:52) saw a Northern Phalarope at Churchill on Hudson Bay "eat the shells as fast as the young emerged," but he suspected his presence may have caused unusual behavior.

The hatchling looked wet and rather bare during the first hour after breaking free of the egg. But during the second hour it dried and became

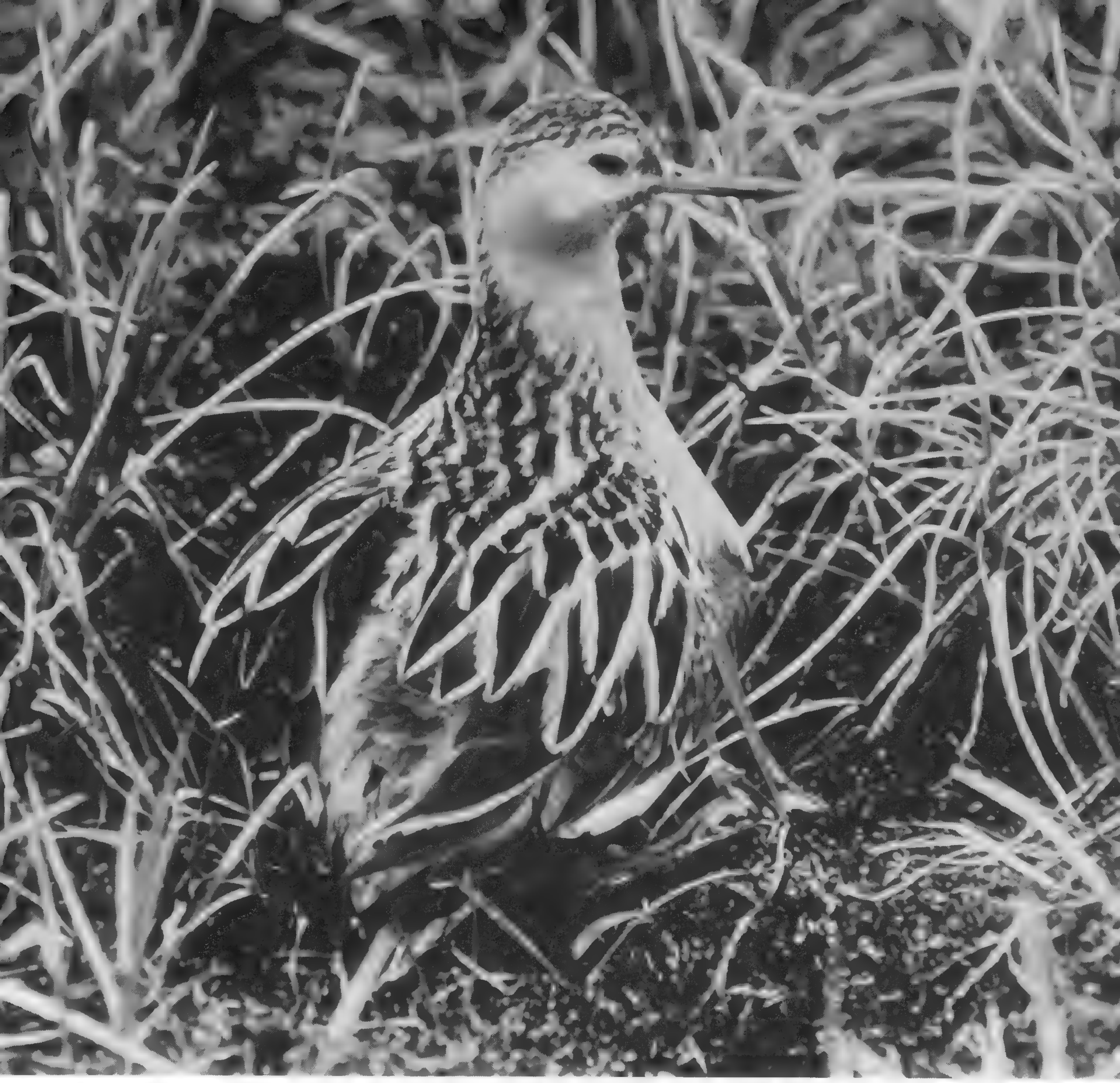


Figure 10. A male, when brooding, spreads his wings and brings them slightly forward to increase the area of shelter for the young.

fluffy and almost indistinguishable from siblings five hours older. Chicks more than two hours old wriggle actively in the nest, peer about with blinking eyes, and peck at vegetation fringing the nest. In the last hours before the young leave permanently, they frequently explore 10 to 30 cm from the nest, crouching outside briefly before returning to the warmth of the male. I suspected this increasing activity of the young prompted the male to lead the brood away from the nest.

The time span between the hatching of the first and fourth eggs in one instance was about nine hours, and departure from the nest occurred at 08:30, about 20 hours after the hatching of the first egg. In the other nest, only three of four eggs hatched, and the departure was less than 15 hours after the hatching of the first egg.

The earliest date for a brood out of the nest was 12 July 1971.

Chicks Out of the Nest

In two instances I watched males depart from the nest with broods, and once came upon a family within minutes after their departure. In all, I followed four broods of known age for a total of 20 hours. For the first three days the male was very attentive; 27 periods of brooding ranged from 3 to 16 minutes, with a mean of 5.8 minutes, and 26 absences ranged from 1 to 7 minutes, with a mean of 3.4 minutes. Thereafter the activity of the young increased rapidly and the amount of brooding declined. On the fifth day, I found the male near the young, but he did not brood them during the hour I kept him in sight, and I did not find this family again. Neither I nor others of our party found males brooding or attending chicks of larger size; so I concluded all contact between parents and juveniles ceased near the fifth day. The males departed from the nesting grounds soon after, before the young learned to fly. This early independence of the young was noted also by Manniche (1910:157) in northeast Greenland and by Lok (1973:215) in Spitsbergen.

In brooding the young, the male spread his wings and brought them forward slightly to increase the area of shelter (Figure 10). Frequently he chose a nook where he could crouch in concealment almost as though on the nest. After a little exposure to chill, the young ran to him and burrowed under his breast, their feet sometimes still visible as they pushed against him. After a minute or two they began to stir and heads popped out here and there through his plumage. Soon one or more burst out and walked away, and before long the male stepped away from any remaining young and flew away.

The warmth of the parent seemed to be the attraction that held the brood together. As soon as a downy chick replenished its body heat, it moved off unhesitatingly by itself. The male sometimes moved among a scattered group and brooded individuals separately, but those nearest usually ran to him. He twittered constantly near them, and his voice probably helped to gather them. When the parent was away, the chicks made no attempt to huddle together, but scattered over an area ten or more meters in diameter. They did not regroup until the male returned, if then. The survival value of this behavior was plain. By withdrawing from the group, the individual enhanced its chance of escaping a predator that found one member.

While watching family groups, I did not see any females in the vicinity. No broods crossed paths, and no male approached a brood not his own. However, females may occasionally show interest in the young. Brandt (1943:155) said he photographed a female Red Phalarope with a young bird in Alaska, and Pierre Lamothe (letter dated 10 May 1972) photographed a male and female with a brood on Bathurst Island 24 July 1969. Bengtson (1968:3) reported "females courting males attending broods as late as 22 July" on Spitsbergen.

When they left the nest, the male led the young, with many pauses for brooding, directly to a pool where the receding water level had exposed a profusion of fresh grassy shoots. Such vegetation zones were not present at the fringe of every pond, but they were quite distinct in appearance, their light green color standing out against the dull hue of the surrounding tundra. Here the young found food and concealment. The chicks picked actively at plant stems, presumably gathering adult chironomids, which filled the stomachs of adult phalaropes feeding in a similar manner at this time.

Chicks less than 12 hours out of the egg scrambled along actively in pursuit of the male, sometimes lagging but catching up when the male stopped to brood. When separated at this time, they called steadily with faint high-pitched peeps. One family made its initial trip of 80 meters from the nest to the feeding ground in less than three hours. The special feeding plots were small in size, usually less than 200 square meters, and the food in one was probably depleted rapidly, for the family always moved in a day or two, traveling hundreds of meters to another if necessary. One family in its third day out of the nest moved 350 meters in two hours.

The food of the young appeared to be extremely specialized, and the availability of it may be a key to suitable nesting habitat. Salomonsen (1950:258) found Red Phalaropes in west Greenland nesting on rocky islets where there were temporary ponds from melting snow. In one instance these pools dried earlier than usual, and he found dead chicks near them.

At this stage the vulnerability of phalaropes to predation is greater than at any other time, and selective pressure must be severe, especially in the High Arctic where cover is sparse. Not surprisingly, the young are adept at concealment. Everyone who has studied them, from Manniche (1910:157) to the present has commented on the difficulty of finding young phalaropes before they begin flying. Hilden and Vuolanto (1972:78) remarked that young Northern Phalaropes "are almost impossible to find" after the first five days and before they begin to fly.

Even the smallest chicks showed fear reaction. They ran or cowered when I approached too close. When the parent gave a sharp note at the approach of a jaeger, they crouched motionless in the grass. In one such instance the male crouched nearby, and the young remained in their separate location until the danger had passed. In another instance the male took flight, calling, when a Long-tailed Jaeger was still at a distance and displayed its distraction flight near the predator while the young crouched in their places.

Small chicks ordinarily did not go into water of swimming depth. When walking the edge of a pond, they walked around the smallest bays instead of swimming across them. However, I suspect they chose their paths not so much to avoid swimming as to stay under cover. When I pursued a two-day-old Red Phalarope into deeper water, it swam buoyantly. Løvenskiold (1964:208) also noted swimming by small young on Spitsbergen, in contradiction to some authors.

On Bathurst Island the earliest brood left the nest on 12 July 1971; whereas Brandt (1943:397) in western Alaska found young out of the nest as early as 19 June.

Red Phalaropes fly when about 18 days old in the Canadian Arctic, according to Parmelee et al. (1967:138) and by 20 to 21 days in Alaska, according to Douglas Schamel (pers. commun.).

Departure from the Nesting Ground

As early as 2 July females began gathering in flocks on lakes and flying high in the air as though about to leave the nesting ground. By 7 July most females had departed, although a few remained at least two more weeks. I was not present when the males and young left, but my associates saw males until around the first week of August and young as late as 26 August. These dates are similar to those reported by Parmelee et al. (1967:139, 141) on Victoria and Jenny Lind Islands 800 km farther south.

Perhaps the departing phalaropes moved first to arctic coastal waters where they were not observed regularly. At Barrow, Alaska large numbers of

TABLE 2

Nest Success

Year	*Total number observed*		*Total number where outcome known*				
			Successful			*Destroyed*	
	Nests	*Eggs*	*Nests*	*Eggs*	*Young*	*Nests*	*Eggs*
1970	8	32	6	24	24*	0	0
1971	18	54	3	11	10	15†	45
1973	15	56	3	11	8	9	35
Total‡	41	142	12	46	42	24	80

*Presumed to have hatched, but young not seen.

†Includes one nest abandoned late in season.

‡Totals do not reveal true clutch size, because some nests were destroyed before set of eggs was complete.

Red Phalaropes, mostly juveniles, gather offshore during August (P. G. Connors, pers. commun.), and north of Siberia at Bennett Island, where they do not nest, they begin to accumulate in late July and become abundant in mid-August (Uspenski 1963:183). Beginning in July the autumn movement spreads far south. Gross (1937:26) found thousands of both sexes on Ungava Bay near Port Burwell, Quebec on 22 July, and Soper (1934:66) saw large numbers in Foxe Channel southeast of Baffin Island in late August. Kumlien (1879:85) encountered flocks 160 km southeast of Cape Cod, Massachusetts on 4 August. The species begins arriving on its wintering waters off west Africa in late August (Stanford 1953:485).

The Pacific flight begins to reach the Farallon Islands off California in July, reaching its peak in late August and early September. Dwindling numbers may remain until November, long after Northern Phalaropes have moved on (David G. Ainley, pers. commun.). The Pacific birds arrive off northern Chile in August (Murphy 1936:995).

In the mid-continent also, Red Phalaropes are the hardiest of the phalaropes, occurring as strays in October and November after other phalaropes and most other shorebirds have passed through.

Reproductive Success

My nest data for three seasons are summarized in Table 2. Of 36 nests with known outcome, 12 (33%) produced young; of 124 eggs laid, 42 hatched. When hatching was due and the nest was found empty but still intact, I assumed hatching took place even though I did not find the young.

Many of these nests, however, were found after incubation was already under way, and therefore the observed losses were less than the true losses. By using the time spent watching all nests, we can calculate the mortality by days and arrive at a better approximation of nest success for the population (Mayfield 1975). The total time covered by observations at all nests was 383 nest-days, and 24 nests were lost; so the nest mortality was $24/383 = .063$ per nest-day, and the survival rate conversely was $(1 - .063) = .937$ per nest-day. The probability a nest will survive 21 days after the first egg (three days for completing the clutch and 18 days for incubation) is $.937^{21} = .25$. Thus, 25 percent of the nests receiving at least one egg may be expected to survive to hatching. Since the success of eggs is only slightly less than the success of nests, about one-fourth of eggs laid produced young; that is, about one chick was produced per year per nest.

The reproductive rate per male may be greater than this to the extent males get second clutches, and the reproductive rate per female will be increased to the extent females produce successive clutches. I cannot estimate the frequency of either of these events, but saw no evidence that either occurs to more than a few birds each summer. On the other hand, the mean annual reproductive rate will be decreased by the proportion of years when very little nesting occurs. Such a season occurred twice in nine years, 1972 and 1974 between 1968 and 1976, for which information is available at this location. Also it appeared some females do not secure mates in normal years.

I was unable to measure either these opposing effects or the loss of young phalaropes between hatching and fledging, a time of great hazard. Still it was apparent the number of flying young seen late in the summer was much smaller than the number hatched in the vicinity, leading us to believe the mortality of young before fledging was at least 50 percent of those hatched. If so, the success of eggs to fledging may have been close to 10 percent in the years of my study at this location.

Kistchinski (1975:299) estimated the reproductive rate of Red Phalaropes on the Indigirka River delta in 1971 by comparing the number of young present 1 to 3 August with the adult population earlier in the summer. He concluded that the "population gain" was 10 to 20 percent.

Production of Red Phalaropes on Bathurst Island was lower than that usually reported for other species of shorebirds elsewhere. Nest success is not known for many species of this group, but generally it appears higher than for most passerine species. For a number of shorebirds, Boyd (1962:383) reported success to hatching from 66 to 96 percent of eggs laid, and survival to fledging from 40 to 80 percent of chicks hatched. Ricklefs' (1969:32) larger samples of arctic shorebirds showed hatching of 70 to 80 percent of eggs laid. However, most recent studies point to high losses between hatching and fledging. Jehl (1973:34) suspected fledging success of Stilt Sandpipers, *Micropalama himantopus*, did not far exceed 50 percent, although the hatching success was 83 percent. Among Dunlins in Alaska, Holmes (1966:25) judged mortality among non-flying chicks to be as high as 50 percent in some years, and mortality in the first year of life to be about 70 percent. Pitelka (1959:257) believed success of Pectoral Sandpipers to fledging was about 25 percent.

Destruction of nests and eggs by predators varied widely from year to year (Table 2). The major agent of nest mortality was the Arctic Fox, *Alopex lagopus*, which was scarce in 1970 when I observed no losses and common in 1971 and 1973 when losses were high. At several robbed nests the foxes left scats. The phalarope's only defense against the fox was concealment, and this was not very effective for nests in such sparse cover. Larger birds, including King Eiders and jaegers suffered even more heavily than phalaropes in 1971, when hardly a nest of those species survived. Although the fox lived mainly on lemmings, it hunted widely and was alert to birds and eggs in its path.

Jaegers, gulls, and owls may have preyed on eggs, but I did not see it. Indeed, I was amazed to see nests survive in areas patrolled regularly by these predators. Perhaps they were a threat mainly to small young. Members of our party saw young shorebirds of other species pursued and taken by jaegers. However, the interactions of predators were complex, and to some extent they offset one another. Foxes reduced the pressure of jaegers by destroying their nests and causing them to leave the area early, and jaegers aggressively defending territories reduced the pressure of other avian hunters. Snowy Owls had the unique ability among birds of this region to repel foxes, and they spread a blanket of immunity for hundreds of meters around their nests.

Arctic Weasels, *Mustela erminea*, occurred here but were too rare to be a factor. Other mammals present included the Collared Lemming, *Dicrostonyx groenlandicus*, Peary's Caribou, *Rangifer pearyi*, Musk ox, *Ovibos moschatus*, Arctic Hare, *Lepus arcticus*, Gray Wolf, *Canis lupus*, and Polar Bear, *Ursus maritimus*. None of these appeared to hold any serious threat to phalaropes or their nests, although lemmings may be disruptive to shorebird nests when extremely abundant (Holmes 1966:24). Their damage to phalaropes on Bathurst Island may be minimized because most of them in summer abandoned the wettest flats the phalaropes favored.

Predators appeared a threat mainly to eggs and non-flying young. I did not see any adults attacked, but instances have been reported elsewhere. On Southampton Island, Sutton (1932:152) found a Red Phalarope in the stomach of a Parasitic Jaeger and saw Peregrine Falcons, *Falco peregrinus* chase them several times. At a beach on Prince Patrick Island, MacDonald (1954:228) saw Glaucous Gulls prey on Red Phalaropes trapped by ice in a late-summer freeze. Manniche (1910:158) reported Gyrfalcons, *Falco rusticolus*, capturing Red Phalaropes on water in northeast Greenland. These falcons are extremely rare on Bathurst Island.

Red Phalaropes and their bird neighbors often got mutual benefit by attacking and distracting common enemies. The most effective defenders among shorebirds here were Black-bellied Plovers, and their high-velocity dives at enemies seemed to gain in effect when combined with the horizontal dashes of phalaropes. Red Phalaropes on Spitsbergen often nest near Arctic Terns (Bengtson 1968:2; Løvenskiold 1964:208), and Northern Phalaropes in Finland do likewise (Hilden and Vuolanto 1972:64). Wilson's Phalarope often nests near Black Terns, *Chlidonias niger*, and Common Terns, *Sterna hirundo* (Höhn 1967:220). This proximity may be a coincidence since both birds nest in the same wet habitat, but the association between the Northern Phalarope and Arctic Tern in northern Europe is so frequent as to suggest the tendency may have evolved under selective pressure.

My mortality data from Bathurst Island may have been biased by my daily presence near the nests, by our camp attracting foxes, or by some other factor; but if my sample was representative, this population needed a remarkable survival rate in the months at sea or recruitment from more productive areas to sustain itself.

Summary

This report is based on three summers of intensive study of the Red Phalarope, on Bathurst Island in the Canadian High Arctic, supplemented by observations of others in additional years. The phalarope nested on extensive tracts of sedge-moss tundra dotted with freshwater ponds. In the best of this habitat the mean density was 4.9 nests/km^2, and the total local population was of the order of 100 birds. The first of the species arrived in mid-June, and some nests were started almost immediately, but others were built over a period of at least three weeks. The pair bond may have been formed almost instantly after the males arrived, but it was broken quickly after the male began incubation. Females then were able to produce sets of eggs with different males (serial polyandry), and a few probably did so. The females have exceptional egg-laying capacity; their eggs are small in comparison to body weight, and they are able to produce successive clutches rapidly and successive eggs in a clutch in less than 24 hours. Both sexes participated in nest-site searching and nest-shaping, but the male alone lined the nest, incubated the eggs (18–19 days), and provided care for the young. Most females left the region very soon after laying eggs, leaving all food resources to the males but increasing the likelihood that a male replacing a lost clutch did so with a different female (serial polygyny), a possibility suspected but not proved. The dependency of the chicks was short, and most males left before their young were fledged. The phalaropes here were subjected to widely fluctuating food resources and predation, and they showed great flexibility in exploiting favorable situations, offsetting years when hardly any phalaropes nested. Thus, the bird was highly opportunistic, adjusting its behavior to get the greatest possible yield from males when conditions were good. The nesting success of this sample, which hatched 25 percent of eggs laid, was lower than that reported for other arctic shorebirds and was probably insufficient to sustain the population without recruitment from more productive regions elsewhere.

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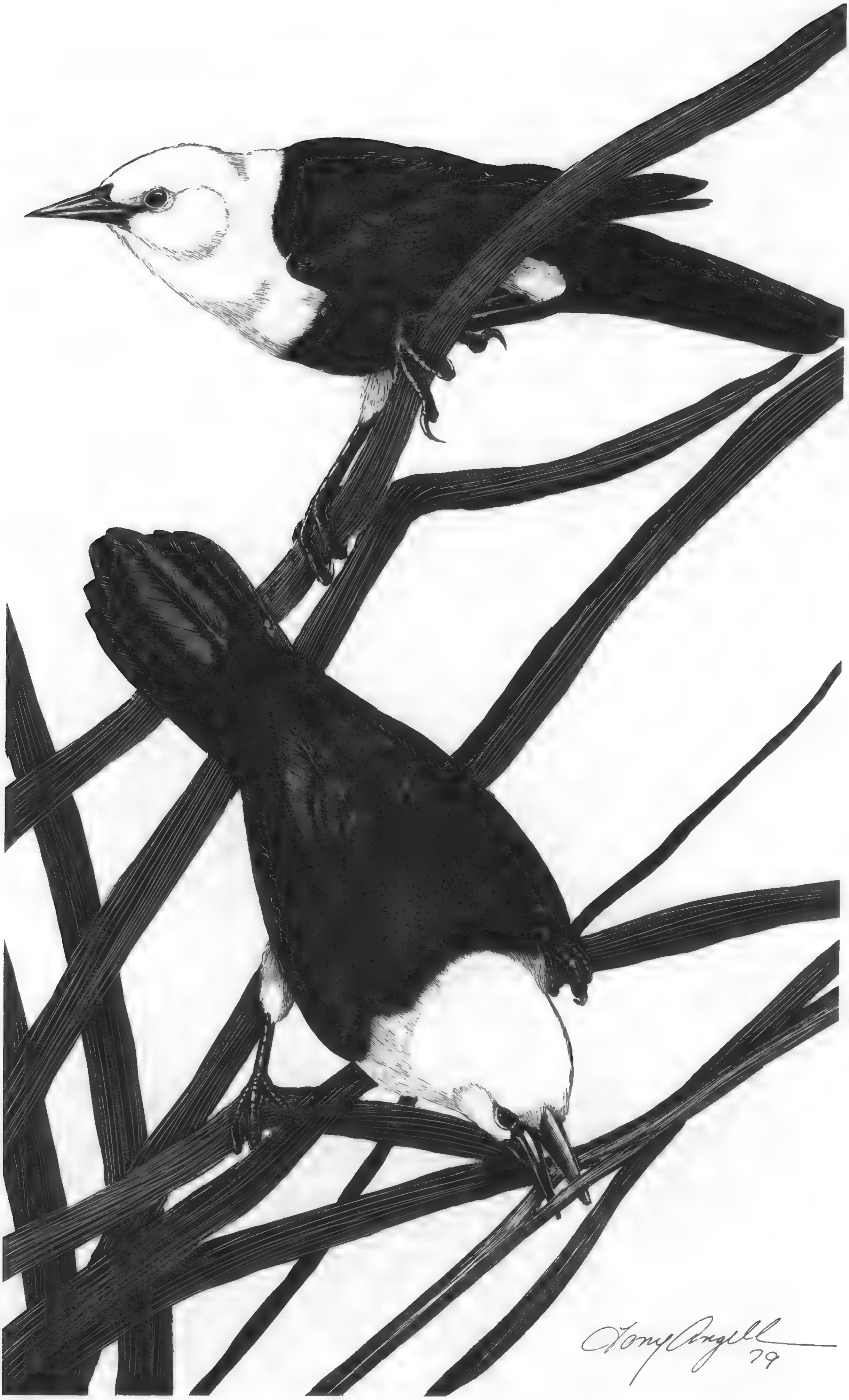
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79

Scarlet-headed Blackbird, *Amblyramphus holosericeus.* Drawing by Tony Angell.

BEGGING BY NESTLING SHINY COWBIRDS: ADAPTIVE OR MALADAPTIVE

MICHAEL GOCHFELD

All recognizable features of organisms represent adaptive compromises between negative and positive selective factors in the environment. Some species do not incubate their own eggs or rear their own young. Instead, they deposit eggs in the nests of other species. The evolution among birds of this phenomenon, called brood parasitism, and the special adaptive features of brood parasites and their hosts have attracted considerable attention and have stimulated speculation both sound and far-fetched. To understand the coevolutionary struggle of parasites and their hosts, it is fruitful to look for special adaptations possessed by parasites, and I consider here the begging behavior of cowbird nestlings as a possible special adaptation improving survival of the cowbird in alien nests. The Shiny Cowbird *(Molothrus bonariensis)*, like its North American relative the Brown-headed Cowbird *(M. ater)*, must deposit its eggs in the nests of other species in order to survive. It occurs throughout most of South America and the West Indies. Hudson (1920) was impressed by unusual behavioral features of nestling Shiny Cowbirds, noting that, unlike most nestling birds, they responded to a great many stimuli by begging vigorously. Nice (1939) described a captive young Brown-headed Cowbird as "phlegmatic" and believed that it possessed no special adaptations, but she did note that it begged freely in response to many stimuli. Ficken (1967) reported on the death of a fledgling Brown-headed Cowbird that had the temerity to beg from a Common Crow *(Corvus brachyrhynchos)*.

During field studies of the behavior and ecology of South American red-breasted meadowlarks *(Sturnella* spp.), I studied their interactions with Shiny Cowbirds and compared the behavior of young cowbirds and meadowlarks, both of which are members of the family Icteridae. Nestling birds compete for the food brought by parents and the diet is ideally adjusted to provide optimum growth for nestlings. The diet of a particular host may not be optimal for parasitic young, and often there are certain features such as behavior or mouth lining color which stimulate adult feeding activity. Parasites with host specificity may evolve such features (Payne 1973) but generalists cannot. Cowbirds could compensate for any such deficiencies by exaggerated begging behavior, thereby presenting hosts with supernormal stimuli. I asked the following questions: Do nestling cowbirds beg more vigorously or aggressively than host nestlings? What are the benefits and risks of aggressive begging?

Study Area and Species

I studied cowbirds and meadowlarks in Argentina in 1970 and 1971 at Estancia La Saudade (37° 45′ S; 62° 26′ W, elevation 370 m), 92 kilometers north of Bahia Blanca, and on the outskirts of Bahia Blanca, on the southern pampas of Buenos Aires Province. In these areas the Loyca[1] or Greater Red-breasted Meadowlark *(Sturnella loyca)*, Pampas Meadowlark *(S. defilippi)* and Shiny Cowbird occurred together (see Short 1968 for taxonomic treatment). Weights of adult males trapped at La Saudade are: Loyca Meadowlark, 84 to 98 grams (mean = 91.4 g); Pampas Meadowlark, 61 to 81 grams (mean = 72.1 g); and Shiny Cowbird, 50 to 62 grams (mean 54.6 g).

Nesting and Parasitism

Pampas Meadowlarks nested mainly in wheat fields and pastures and, of 11 completed nests found, none were parasitized; but the species has been parasitized elsewhere (Withington 1888, G. H. Orians, pers. commun.). The Loyca Meadowlark nested almost exclusively in fence rows and 23 and 24 completed nests (96%) contained cowbird eggs or young. This high percentage is not unique. All the nests of Yellow-shouldered Blackbirds *(Agelaius xanthomus)* found by Post and Wiley (1977) in eastern Puerto Rico were parasitized. So were all the nests of the Rufous-collared Sparrow *(Zonotrichia capensis)* found by King (1973) in northwestern Argentina at the height of the cowbird's breeding season. Over much of the cowbird's range, this sparrow is the most frequent host (Friedmann 1963, King 1973, Sick and Ottow 1958). However, I found only 2 of 13 sparrow nests parasitized on the pampas. Several studies (King 1973, Mayfield 1960, Nice 1937) document monthly and yearly variation in parasitism rates for various hosts of both Shiny and Brown-headed Cowbirds, so we can assume that the frequencies of parasitism reported here are not typical for these hosts elsewhere in their range or at other times.

The placement of Loyca Meadowlark nests near fences apparently provided cowbirds with convenient perches for nest-finding, and I attribute the high rate of parasitism on this meadowlark to nest placement (Gochfeld, in press). Friedmann et al. (1977) provide a recent account of Shiny Cowbird-host relations.

While examining Loyca Meadowlark nests, I noted that cowbird nestlings, even with eyes closed, usually begged loudly and insistently when I parted the vegetation over a nest, whereas meadowlark nestlings generally did not. Older cowbird nestlings with eyes open (four to five days) aggressively thrust their heads and necks upward, climbed over their nest mates and gaped repeatedly with loud begging calls. These begging notes were of higher intensity and less discrete than location notes uttered by young birds in the absence of parents. The calls accompanied begging and were not associated with escape or crouching behavior.

Observations on Captive Broods

I studied the behavioral differences of the nestlings by hand-rearing the following combinations of birds taken from nests at the ages indicated: one

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[1] Loyca is an Amerindian name widely used in Argentina and Chile to refer to *Sturnella loyca*. The Americanized form Loyca Meadowlark, used here, has been inserted editorially to clarify its relationship to other meadowlarks.

Loyca Meadowlark (4 days old) and two cowbirds (4 and 5 to 6 days old); one Loyca Meadowlark (6 days old) and one cowbird (6 to 7 days old); one Pampas Meadowlark (5 days old) and one cowbird (4 to 5 days old).

All birds had their eyes open and could direct begging toward the food (cf. Tinbergen and Kuenen 1939). The broods were raised in covered 10 × 10 × 15 cm wooden boxes, and were fed with forceps at two- to five-hour intervals. The food was a mixture of three parts powdered dog biscuit, one part fresh shredded lamb, one part egg white, and one part powdered milk. I also added multiple vitamin supplement. I mixed the food with just enough water to form firm pellets.

All cowbirds, even from four days on, gaped and vocalized when the box was opened. Six-day-old cowbirds stood, climbed up on other birds, and jabbed vigorously upward with the bill. When seven to eight days old, begging was accompanied by wing fluttering. Cowbirds begged continuously until four to five food morsels were given to them. Meanwhile, meadowlark chicks, even though they were usually slightly larger than the cowbirds, remained crouched and silent, gaping only when I touched them with forceps.

After three days the meadowlarks began to beg more because of the lessening of their fright responses and also because of conditioning, whereby they learned to associate opening of the box with food. Meadowlarks vocalized much less than cowbirds. On four of seven occasions when feeding was delayed beyond five hours, I heard spontaneous begging notes from cowbirds as I entered the room.

Observations at Parasitized Nests

Since it is difficult to observe a female meadowlark as she carries food through the dense vegetation near the nest, I monitored the volume and duration of begging calls remotely, using a Uher M-514 microphone near the nest, and a 42 meter cable to a Uher 4000 L Report recorder in my blind. I timed duration of calls and measured amplitude on the record-level meter. I studied three Loyca Meadowlark nests containing the following: three Loyca Meadowlark and one cowbird chicks (all five to seven days old); two Loyca Meadowlark and two cowbird chicks (all four to six days old); one Loyca Meadowlark and two cowbird chicks (all six to seven days old). I monitored each nest for three to four hours during the early afternoon. I recorded data on four consecutive feeding visits with both meadowlark and cowbird chicks present, on four consecutive visits after the cowbirds were removed, and on four more visits when cowbirds were replaced and meadowlarks removed. In the third nest I also recorded data for four additional visits with all nestlings back in the nest.

Including my manipulations, the observation periods for each set of four visits lasted 32 to 68 minutes. Thus some nestlings were deprived of food for that length of time.

The data (Table 1), though few in number, were suitable for a within-nest analysis (Mann-Whitney test). The hypothesis in each case is that the intensity and duration of begging by the two species do not differ significantly. In all cases, however, begging was longer and louder when cowbirds were in the nest. Removal of meadowlarks had little effect on the intensity of cowbird calling and none on the duration. For the three nests combined, cowbird and meadowlark begging were significantly different in both intensity and dura-

TABLE 1

Intensity and Duration of Begging Calls at Three Meadowlark Nests

	Nest 1	*Nest 2*	*Nest 3*
Contents:			
Number of meadowlark chicks	3	2	1
Number of cowbird chicks	1	2	2
Experimental condition:			
I All birds present			
Intensity	4 4 4 4	4 3 4 3	4 3 4 4
Duration*	15 18 20 15	18 14 12 18	10 14 12 16
II Meadowlarks Only			
Intensity	2 3 2 3	2 1 3 2	2 1 1 2
Duration	9 10 11 8	11 7 5 8	2 8 7 8
III Cowbirds Only			
Intensity	4 4 4 4	4 3 4 4	4 4 3 2
Duration	14 19 14 12	12 15 16 17	11 13 15 14
IV All birds present			
Intensity			4 4 4 4
Duration			12 13 14 11
Compare II vs I or III			
Mann-Whitney U	U=0, p=.014	U=1, p=.029	U=0, p=.014

*Time measured in seconds.

tion (p<.011 for both measures). This may partly reflect the fact that cowbirds had been deprived of food for almost an hour before they were put in nests alone. Data from the third nest show that the intensity of vocalizations relate mainly to the presence or absence of cowbirds rather than merely to their removal.

Discussion

Observations at nests and on captive birds show that young Shiny Cowbirds show unusually aggressive and vigorous begging behavior, at least in comparison to their meadowlark hosts. Such behavior may be a special adaptation to monopolize food brought to the nest. Payne (1973) discussed how indigo bird (*Vidua* spp) nestlings have a pattern of begging behavior which mimics that of their fire finch (*Lagonosticta* spp) hosts. Such behavior, essential for survival in host nests, would be maladaptive in the nests of other species. Since Shiny Cowbirds are not species-specific in their parasitism and cannot be specialized on a narrow range of hosts, they must exhibit begging behavior suitable over a wide range of hosts.

The exaggerated begging of Shiny Cowbirds includes begging in response to a wide variety of stimuli, perhaps indicating a low threshold for begging. The begging calls are louder, more insistent, than those of its nest mates, and are often accompanied by aggressive head-thrusting, climbing, and gaping. In my captive broods, the cowbirds always presented better targets for my forceps than did the meadowlarks, even though the latter were larger. It remains to be determined whether an adult meadowlark with food interprets this behavior in the same way. It is possible that such aggressive begging behavior is more likely to occur in the presence of a large host species like the Loyca Meadowlark, in which adults weigh almost twice as much as cowbirds, than in nests of smaller, more easily out-competed hosts.

Possible Hazards of Aggressive Begging

The apparent advantage of vigorous begging is not without associated risk. For one thing, the host might single out atypical begging behavior and ignore it, thereby favoring its own young. Although such selective feeding might be advantageous to the host, the linkage between begging and parental feeding may be so strong that selective feeding cannot evolve (see Hamilton and Orians 1965).

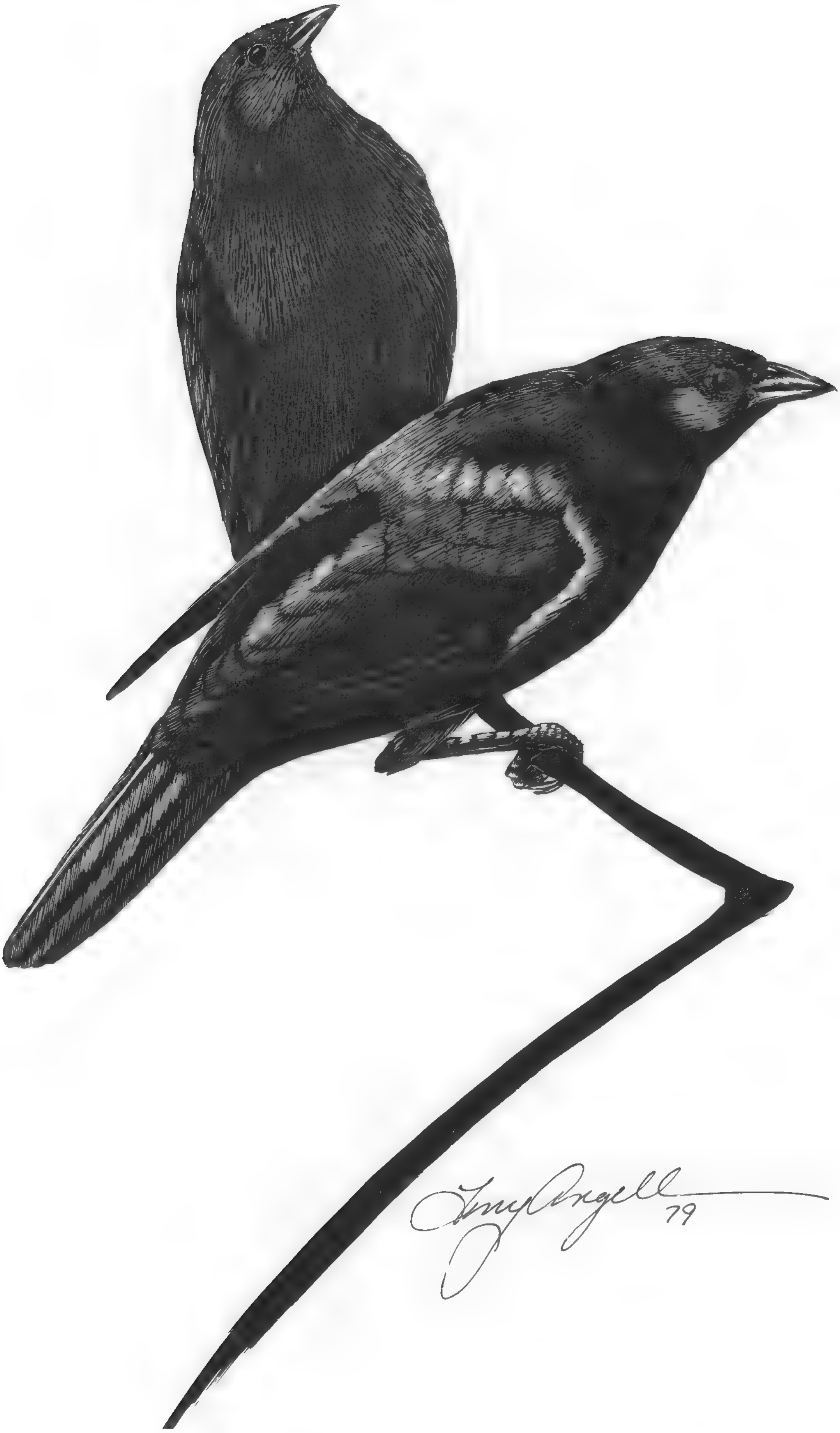
Although it is beneficial for a nestling to beg vigorously when food is at hand, it is advantageous to be silent at other times to avoid attracting predators that orient acoustically. Young cowbirds, however, seem indiscriminate in their begging behavior (Ficken 1967, Friedmann 1929, Hudson 1920). Hudson (1920) reported the loss of otherwise inconspicuous nests of several Argentine species, blaming noisy cowbird nestlings for revealing nest locations to the predators.

Like other field workers (Lanyon 1957, Marchant 1960), I had difficulty locating meadowlark nests since they are usually well-concealed in dense vegetation. I relied on discovering nests when adults made feeding visits; but female meadowlarks are very careful and often land several meters from the nest and walk through the grass. So while I could find the general area of the nest, I had considerable difficulty in locating the nest itself. On several occasions my work was facilitated by the begging calls of nestling cowbirds. The calls were apparently elicited by my footsteps. When I parted the vegetation over such nests I could sometimes actually see the young cowbirds alternately gaping and calling, while their meadowlark nest mates lay silently with heads retracted. I was able to induce begging by cowbirds by stamping my foot about a meter from the nest, while meadowlarks responded sluggishly or not at all. Although the meadowlarks did not beg readily in response to my footsteps, they immediately began uttering high intensity alarm notes (cf. Driver and Humphries 1969) when grasped.

Possible Biases in Nest Finding

It is possible that the Loyca Meadowlark nests I was able to find just happened to be ones that cowbirds were able to find, for there were some meadowlark nests I was never able to discover. Unparasitized nests might remain undiscovered for two reasons. Either they are so well hidden that neither cowbirds nor I could find them, or there are no noisy cowbird nestlings to give the site away. I doubt that such bias significantly affected my study, since I found the well-hidden but unparasitized nests of the Pampas Meadowlark and many Loyca Meadowlark nests which had cowbird eggs but no cowbird young.

Berger (1951) noted that there is no evidence that nests which seem well-hidden to humans are also well-hidden from cowbirds. An important question is whether nests well-hidden from the latter are also well-hidden from predators; or conversely, whether nests which cowbirds find and parasitize are ones that predators also are likely to find, even without noisy cowbird nestlings being present. If, in addition to finding "easy" or predator-prone nests, cowbirds further jeopardize the safety of host nests by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79

Shiny Cowbird, *Molothrus bonariensis*. Drawing by Tony Angell.

noisily advertising their location, one could easily account in part for the low overall reproductive success ascribed to both Brown-headed and Shiny Cowbirds (Berger 1951, Hudson 1920, Young 1963). Selection should place a premium on cowbirds finding nests that are well-hidden from predators.

Although selection could promote more "careful" nest-finding behavior by cowbirds, the vigorous begging behavior may be so critical to survival that it may be hard to select against in any way. An additional hazard faced by cowbirds in meadowlark nests is the relatively high nest loss due to livestock (Gochfeld 1975, Lanyon 1957, Roseberry and Klimstra 1970). Loud begging calls might deter, or attract approaching livestock, but it is not known whether cow and cowbird can communicate in this fashion.

Predation on Parasitized Nests

Except for my own "predation" on nests I discovered due to noisy cowbirds, I did not observe natural predation of parasitized nests. Hudson (1920) did report such predation, particularly by the Chimango *(Milvago chimango)*, which he said was able to find well-hidden nests of several species due to the noisy cowbird nestlings. Data on differential predation on parasitized and unparasitized nests are scant. Mayfield (1960:198) reported on 86 unparasitized and 58 parasitized nests of Kirtland's Warblers *(Dendroica kirtlandii)*. The former had a 7 percent loss to predators and a 19 percent overall loss, while the latter group lost 22 percent of its parasitized nests to predators, and suffered an overall 48 percent nest loss. Parasitized nests fared significantly worse ($p<.01$ for predation and $p<.001$ overall, Chi Square test) than unparasitized nests. Part of the difference may simply reflect the fact that cowbirds tended to find more vulnerable nests. Nonetheless future field work focused on this aspect of parasitism might be very illuminating.

My observations on cowbird fledglings on the pampas provide additional circumstantial evidence. All three of the young Shiny Cowbirds I saw were being fed by Rufous-collared Sparrows. I also noted 28 Loyca Meadowlark broods, none of which had any cowbirds. Considering the high degree (96%) of parasitism of meadowlark nests in the same area, this suggests that cowbirds suffered much higher mortality rates than the meadowlarks. Unlike Ficken (1967) and Hudson (1920), I did not observe actual predation on cowbirds, but field workers should be alert to this.

Host Suitability

Friedmann et al. (1977) noted that of the 176 species known to have been parasitized by Shiny Cowbirds, only 35 are known to have raised cowbirds successfully. Many of the species records are known only from egg collections, so that fledging could not have been observed, and many other species have been parasitized only rarely. Nonetheless, many of the regular hosts are not known to be ultimately suitable for cowbirds since there is no evidence that they have reared cowbirds to independence. Rothstein (1976) considered in detail how parasites might judge the suitability of hosts and why they regularly lay in nests of unsuitable hosts. He suggests, among other possibilities, that cowbirds do not have the genetic potential to develop an optimal system of host choice that would result in parasitizing only suitable species.

Host suitability can be divided into three stages. Primary suitability refers to species that are common and readily available and whose nests can be discovered without excessive investment of time and energy. Secondary suitability refers to hosts that do not thwart parasitism by ejecting eggs, deserting nests, or otherwise countering the parasite. Ultimate suitability refers to the ability to actually raise parasitic young to independence. Hosts whose diet or behavior are unsuitable for cowbirds or whose nests are readily discovered by predators are clearly unsuitable. At present we must judge unsuitability by the lack of evidence of suitability. Although all forms of meadowlarks have been parasitized, only recently has there been any report of one raising a cowbird. P. F. Elliott (cited by Friedmann et al. 1977) reported an Eastern Meadowlark *(Sturnella magna)* successfully rearing a Brown-headed Cowbird.

It is not clear why cowbirds were successfully reared by Rufous-collared Sparrows but not by Loyca Meadowlarks. Perhaps being raised by a larger species presents a parasite with more difficult intrabrood competition, thereby leading to more vigorous begging behavior with its hazardous consequences. Or meadowlark young may outcompete cowbirds for food in some nests. It would have been valuable to make comparable observations on cowbirds in sparrow nests.

Since cowbirds fared so poorly in meadowlark nests, one wonders why the parasitism rate was so high. Perhaps cowbirds were simply focusing attention on a large, conspicuous species. Since Loyca Meadowlarks nested near fences, cowbirds were able to discover nests with relative ease. An individual cowbird might simply learn that it "pays off" to look for meadowlark nests. One mechanism for host selection, imprinting on ones' foster-parent, offers parasites a good way of choosing ultimately suitable hosts. However, since there are few, if any, meadowlark-reared cowbirds, this mechanism does not account for the high rate of parasitism.

On Being a Generalist

Host-specific parasites, once they have perfected their species-specific adaptation, are insured against making the kind of mistake that Shiny Cowbirds seem to be making by parasitizing Loyca Meadowlarks. Although it is tempting to think of non-specific parasites as being primitive or unspecialized, there are several reasons for viewing non-specialization as an adaptive strategy in its own right. The current system of host choice by generalists such as Shiny and Brown-headed Cowbirds is very flexible. Although the system breaks down in some cases, such as the high rate of parasitism of Loyca Meadowlarks, its overall success must be judged by the rapid expansion in range and abundance of both species (Friedmann 1963:5; Post and Wiley 1977). These species are buffered against severe oscillations in host populations and also can exploit opportunistically new potential hosts with which they come in contact.

Moreover, a host-specific parasite may seriously interfere with its host population to its own detriment. A generalist may drastically affect the population of some hosts, particularly naive species like the Kirtland's Warbler (Mayfield 1965, 1977), yet maintain high population levels through the ability to exploit many other species as well.

Summary

During two field seasons on the Argentine pampas I found the Greater

Red-breasted Meadowlark or Loyca Meadowlark *(Sturnella loyca)* to be the most frequent host of the Shiny Cowbird *(Molothrus bonariensis)*. In mixed broods, cowbird chicks begged more vigorously than meadowlark chicks, standing, gaping, and jabbing aggressively while uttering loud begging calls. Meadowlark chicks, by contrast, appeared fearful and begged less aggressively and less noisily. The observations are consistent with the idea that, as a generalist brood parasite, cowbirds engage in more vigorous begging behavior than hosts in order to monopolize food brought to the nest. Such an adaptation can function in nests of many different hosts. Such behavior may be particularly important when the host species is large. Cowbirds also tended to beg even when no food-bearing adult (or person) was present, and I found three meadowlark nests by following the begging calls of cowbirds. Such behavior is maladaptive by enhancing the risk of nest discovery by predators.

On the study area, adult cowbirds were abundant and there was a high frequency of parasitism on meadowlark nests, but no young cowbirds were raised by meadowlarks. The differential mortality of cowbirds and meadowlarks may be due to predation, as other field workers have observed. Some cowbirds were raised by Rufous-collared Sparrows, although the parasitism rate in the study area was low. Further study on behavioral development of hosts and parasites would provide a clearer picture of the exaggerated begging behavior of cowbirds. Comparison of the behavior of parasitic young fostered by different host species would be particularly valuable.

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DISPLAY AND RELATED BEHAVIOR OF THE WIRE-TAILED MANAKIN

PAUL SCHWARTZ AND DAVID W. SNOW

Although among the most strikingly colored birds in a family that includes some quite handsome ones, the Wire-tailed Manakin *(Pipra filicauda)* has teased the imagination of ornithologists because of another attribute, a uniquely modified tail quite unlike that of any other manakin, with no close parallel in any other bird. The shafts of the rectrices are prolonged into fine wire-like filaments curving inward and downward, those of the outermost pair being longest and the others progressively shorter (Figure 1). The filaments of the outermost rectrices of adult males, if straightened, may be up to 50 millimeters in length, about half as long as the head and body combined.

This peculiarity of the tail was long considered to be of sufficient taxonomic importance to warrant placing this manakin in a monotypic genus, *Teleonema* or *Cirrhipipra*; but Haffer (1970) has shown that it is one of a group of three very closely related parapatric species which he combines in a superspecies (see *Terminology*). In the other two species, the Crimson-hooded Manakin *(P. aureola)* and the Band-tailed Manakin *(P. fasciicauda)*, the tail is unmodified (for illustrations see Parkes 1961: opp. p. 345, and Sick 1967a: opp. p. 12). The ranges of the three species cover much of northern and central South America east of the Andes, the Wire-tailed Manakin occupying the sector from the Rio Purus and the Rio Branco in Brazil westward to the Andes, with a northward extension along the eastern base of the Andes in Colombia to western and northcentral Venezuela. Haffer (1970) gave reasons for supposing that the differentiation of these three species from a common stock may be quite recent, perhaps dating from a period in the quaternary when the forests of Amazonia were reduced to a number of isolated refuges. If this is so, the Wire-tailed Manakin's tail is an example of rapid evolution of a secondary sexual character. It is of obvious interest to know whether it is associated with a special display, and, if so, how the display is related to those of the other two species in which the tail is not modified. Something is known of the displays of the Band-tailed Manakin (Sick 1959, 1967a) and the Crimson-hooded Manakin (Snow 1963a, where it is called Orange-headed Manakin), but nothing has been reported of the display of the Wire-tailed Manakin.

From May 1975 to June 1978 we were fortunate to make repeated observations of the Wire-tailed Manakin under diverse conditions in Venezuela. We describe here the basic display behavior and its most usual and noteworthy variations, hoping to satisfy in part the long-standing curiosity about these morphologically peculiar and rather astonishing little birds.

This paper was one of the last writing endeavors by the senior author. On 24 April of this year, Paul Schwartz died of a heart attack in Caracas, Venezuela. He contributed greatly to avian systematic problems of northern South America, where he lived and carried on field studies for many decades. His death leaves a void that will not be easily filled.

Methods

Observations within display grounds were made directly both with and without blinds. In the early stages we sometimes sat within eight or ten meters of a main display perch. It gradually became apparent, however, that although display-area owners seemed in no sense disturbed by our presence during the active breeding season, visiting birds, and also owners during other seasons, were partially to considerably inhibited in the manifestation of their usual behavior. Therefore, in later observations we chose posts located strategically to permit normal behavior by the birds while still allowing us an adequate view of their activity through openings in the intervening foliage.

Recordings were made with a Nagra IV tape recorder and a Sennheiser MKH-405 condenser microphone, usually mounted in a 90 centimeter parabolic reflector. With the gain of the recorder appropriately set, all the sounds of a display session registered sufficiently to permit subsequent analysis of events, aided by notes recorded simultaneously and others written separately.

For graphic analysis the recordings were reproduced by the same recorder to a Model 6061-A Sona-Graph using the FL-1 equalization. The sound spectrograms (sonagrams) used to illustrate this article were made at normal speed and with a 150-Hz band-pass filter.

For examination and color banding, birds were captured with mist nets. Such activity was limited to the final day or two of a visit so as not to disrupt the birds' behavior during the main

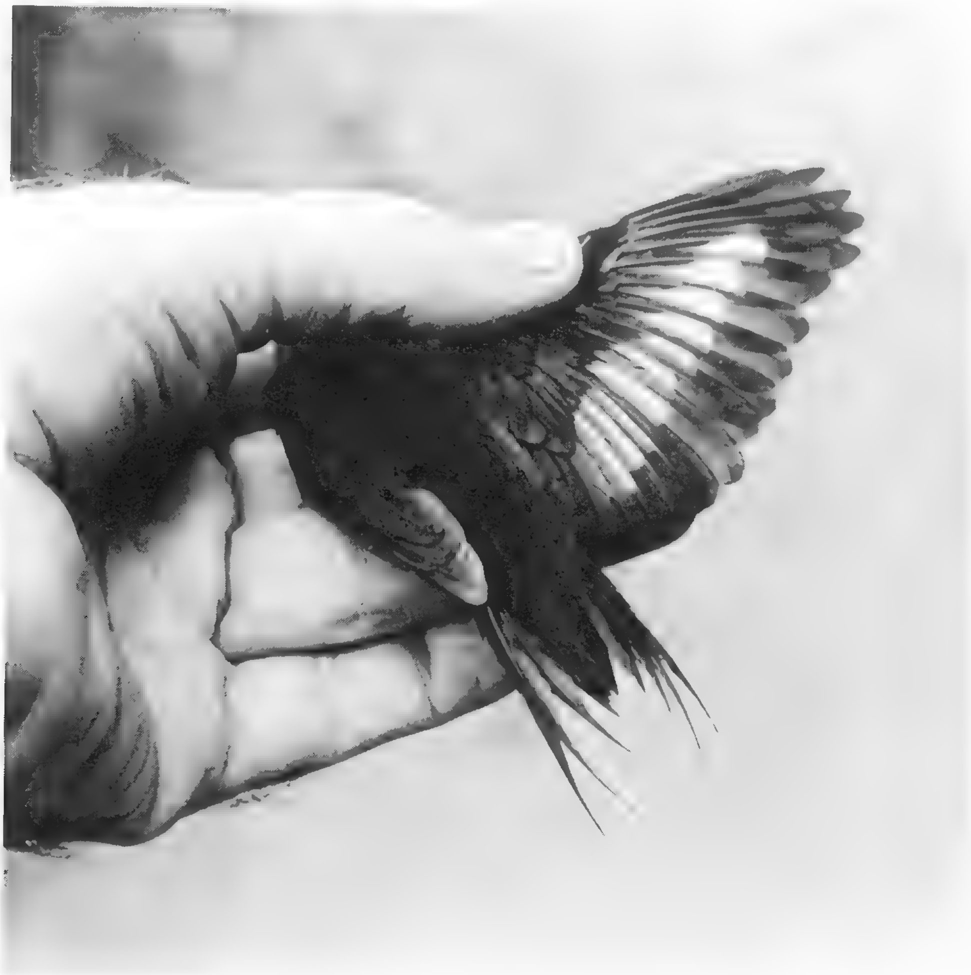


Figure 1. *Above*: Adult male Wire-tailed Manakin held to show the normally concealed white wing patch and the inward and downward curving, graduated tail filaments. In normal closure, both at rest and during display, the tail is not spread as it appears in this photograph. *Below*: Adult male Wire-tailed Manakin on a main display perch. Attracted to the perch by the playing of a recording of his calls and Kloks, he is seen searching the canopy for the "visitor." The mistletoe seeds adhering to and dangling from the perch were regurgitated by the manakin and wiped from his bill onto the perch; mistletoe is not a frequent food of this species. The vertical twig at the right side of the photograph was sometimes used by the former owner of this display area as a substitute "partner" during his Twist display.

periods of observation. During these observations many birds not previously banded could be identified individually from plumage characters peculiar to each.

Observation Periods

Main study area, near Guanare, Portuguesa: 7, 8, 17 May 1975; 10 to 14 May, 25 to 29 September 1976; 2 to 13 June, 26 to 31 August, 11 to 13 September, 24 to 28 November 1977; 19 to 24 March, 18 to 28 April, 18 May to 1 June, 12 to 22 and 25 to 29 June 1978.

Other locations: near Guanarito, Portuguesa, 10 February 1976; upper Rio Masparro region, Barinas, 16 and 17 February 1976; upper Rio Bocono region, Barinas, 19 and 20 February 1976; near Ocumare de la Costa, Aragua, 5 May, 2 July, 3 August 1977.

Terminology

As the reader may find the specific words and terms used for the components of display behavior confusingly numerous, we list them, and a few general terms, with a brief definition; the detailed descriptions are given in the appropriate sections of the article.

General

Allopatric: occupying different geographical areas.

Parapatric: occupying different, contiguous geographical areas. Parapatry is a particular case of allopatry; it usually carries the implication that the biological forms involved are mutually exclusive because of ecological competition.

Superspecies: a group of entirely or essentially allopatric species believed to be more closely related to each other than any one of them is to other congeneric species. The component forms would be treated as a single polytypic species were it not that they are believed or known to have evolved to reproductive isolation, hence to full species status.

Display area: a portion of the woodland claimed by an individual male as a territory in which he displays, and into which he accepts females and potentially cooperative male display partners.

Display perch, or *main perch*: one or more of the perches in a display area, preferred over others for the main display activity.

Auxiliary perch: one or more perches close to the display perch, also used during displays.

Sounds

Call (eeew): restricted in this article to a monosyllabic, downwardly inflected vocalization used for advertisement and contact (see Figure 3a to 3h).

Answer-call: a shorthand expression to denote a call by one bird and the immediate response by another (Figure 3d and 3h).

Pass-by Call (eeeo): a vocalization uttered when a bird on the return part of a Swoop-in Flight passes by the main perch (Figure 6a to 6d).

Culminating Call (eeeooo): given when a bird on a Swoop-in Flight deviates to the main perch instead of continuing to an auxiliary perch; it is essentially a prolonged Pass-by Call (Figure 6e to 6g).

Conflict Whistle (swee): a fairly short upwardly inflected whistle used when males are competing for control of a display area (Figure 4a to 4d).

Appeasement Whistle (sweeee): a longer whistle indicating lack of aggressive intent (Figure 3e to 3h).

Klok: a two-part sound produced apparently by the wings as, or just

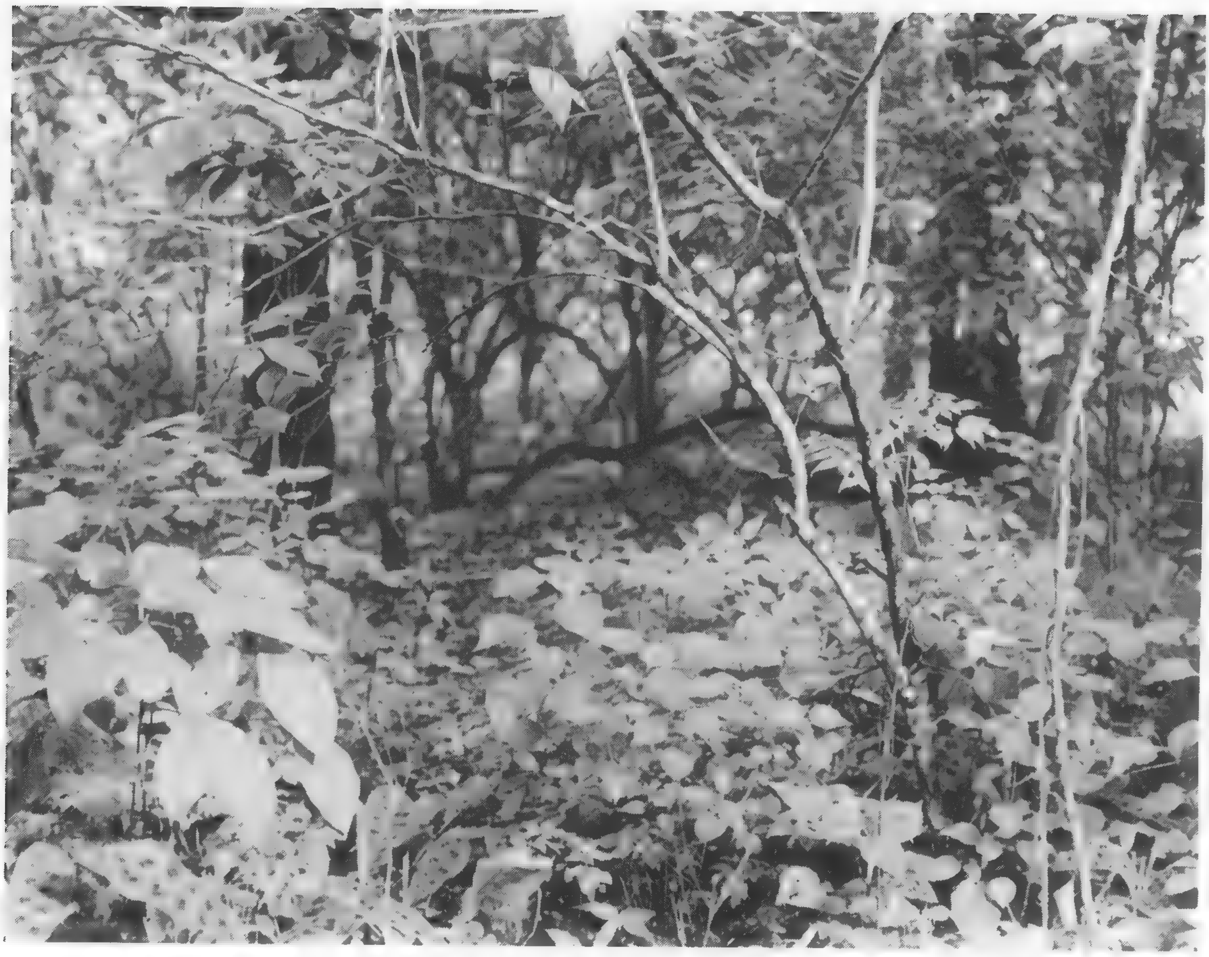


Figure 2. Part of a Wire-tailed Manakin display area (DA-4 in the main study area; photograph taken in early June, the rainy season). The relatively open understory is typical of display areas. The small arched branch in the upper center foreground was a favorite sentry and loafing perch of the owner of this display area. This branch is not suitable as a display perch because the branches immediately above it impede normal execution of the Swoop-in Flight.

after, the bird alights on a perch, or sometimes in the course of a Swoop-in Flight (Figure 6h to 6k).

Kloop: a short burst of very low frequency sound produced by the wings in a Swoop-in Flight (Figure 6m and 6n).

Movements

Side-to-side Jump (usually abbreviated to *Side-jump*): a quick jump to one side and back, performed as a signal and invitation by the jumping bird for another to join it on a display perch.

Stationary Display: a particular stance preliminary to, or transitory in, other displays.

Butterfly Flight: a conspicuously slow mode of flight with shallow wing beats and with wing feathers spread to display the white wing patch.

Twist: the Wire-tailed Manakin's unique *pièce d'occasion*; a brief definition would be inappropriate.

Breakaway: a sudden departure from the display perch with a rapid turn of the body in a curving trajectory downward and away; it is sometimes accompanied by a loud beating or snapping of the wings.

Swoop-in Flight: a particular, ritualized display flight away from, and back to, the display perch.

Flutter: an awkward appearing maneuver with the bird seeming to lose balance on the perch and trying to regain it with fluttering wings.

Habitat

Our observations were made in the southeastern foothills of the Venezuelan Andes, in the lowlands of the llano, and on the north side of the Cordillera de la Costa. We found the Wire-tailed Manakin only in woods that are largely or entirely evergreen. In regions of seasonally deciduous forest, therefore, it seems to be limited to those portions along water courses.

Our main study area is located about 25 kilometers northeast of Guanare, Portuguesa, about 200 meters above sea level where the llano adjoins the Andean foothills. The forest in this area is broken, with extensive grasslands and natural savannas devoted to cattle raising. A small stream meanders through the general display grounds. Except for a few higher emergents, the trees are mostly not over 25 meters tall. The ground varies from bare to moderately populated with herbaceous growth. The understory may be completely clear below two to four meters, except for a sparse to moderately dense scattering of saplings and vines. This layer is mostly woody, with tree stems of various sizes and scattered shrubs; foliage is relatively scanty (Figure 2 and 12).

Display Areas

Requirements for display areas include a fairly open understory, with saplings and vines providing perches appropriate for display, and an adequate food supply in the immediate vicinity. In the more dense forests, the display areas are near the edge of water courses, natural clearings, or man-wrought alterations. Individual display areas are irregular in outline but usually longer than wide, varying in size from about 20 × 10 to 35 × 25 meters. They may be within sound of each other but are not necessarily so. Although sometimes fairly close, in our experience they are never contiguous.

An owner uses many perches throughout his display area, most of them being between one and five meters above ground and with diameters from 4 to 20 mm. Some of these perches are used more than others, and for the main display usage narrows to only a few, one of which is usually preferred. Twelve display perches measured from 1.4 to 2.3 meters high, with diameters from 4 to 11 mm, and were horizontal or inclined to about 15 degrees (Figure 1). One secondary display perch used fairly frequently was angled about 35 degrees. This was very unusual, for such an inclination is not convenient to the birds' behavior.

Further requirements for display perches are that they be free of foliage and obstructing twigs for 40 cm or more, with suitable auxiliary perches within one to three meters, and that they offer a relatively clear flyway in front and for a short distance behind.

Plumages

The adult male is feathered in a striking combination of rich yellow, scarlet, and velvety black. All but the outer primaries and innermost secondaries (tertials) are broadly white on the inner web; this shows as a white band when the wing is extended but is concealed when the bird is at rest (Figure 1). The iris is white, the legs bluish purple.

In most illustrations of this species, the tail is misleadingly shown as fanned so that the filaments form a lyre-shape. We have never seen the tail so displayed; it is always closed and usually looks like a skinny brush that has seen better days. At times the filaments of the two halves of the tail cross neatly to form a lattice or, when the tail is compressed, diverge into a delicate fan-shape; but these forms have no special display function that we can detect and appear to be of accidental occurrence.

Todd (1928) separated a northern form of the Wire-tailed Manakin under the name *subpallida* mainly on the basis of slight color differences on the underparts, the yellow being paler than in the typical form from western Amazonia, especially on the belly, and extending further back so that the tibial feathering is mainly pale yellow and not black as in the typical form. Northern birds are also a little longer-winged. We mention these slight geographical differences only because there is another difference between the two populations which is relevant to the display and which Todd did not mention. In northern birds the tail filaments are sharply graded in length from outside inwards, that of the fourth feather from the outside being only slightly prolonged; in Amazonian birds the three outermost feathers are of nearly equal length and the fourth is only 10 to 12 mm shorter than the third.

Females are plain olive-green above and paler yellowish olive below. For the most part, the tail filaments are appreciably shorter than in the adult male. Occasional females have filaments about as long and well developed as in the male. Rarely, a female may possess other male characters such as a few scarlet feathers in the crown, a yellowish frontal band, underparts more yellow than normal, and a partially developed white wing patch. In some museum specimens, the iris color is given as white, in others as brown; there may be both individual and age variation as in the Golden-headed Manakin, *Pipra erythrocephala* (Snow 1962), but all birds known by us to be adult females had white irises with little or no brownish tinge. The adult female's legs are dark lilac, as in the male.

Young males in juvenal plumage are similar in color to females and have brown eyes; but in a more advanced stage of immature plumage they have brighter yellow underparts, a yellowish frontal band, and white irises. At this stage the tail filaments are as long, or nearly so, as the adult males'.

Sounds

The Call

The unmodified word "call," as used in this paper, refers to the vocalization most frequently uttered by the Wire-tailed Manakin under normal conditions. Although it serves as advertisement, it is not loud and is unlikely to attract other birds from any distance. As display areas are well known to the local population, the call's main function seems to be to indicate that a display area is occupied. The call serves also as vocal contact between the owner of a display area and visitors. For the most part, a visiting male does not enter a display area haphazardly but comes with the intent of joining the owner in display and announces his arrival with a call. The owner answers with a similar call, usually immediately. Infrequently, because the owner is loafing in a far corner of his display area or is absent briefly, the visitor may call another time or two before the owner hears and answers. It also may happen that the owner is calling actively when a visitor arrives and the visitor answers the owner's call; but often during the early part of a visitor's presence, the owner calls first. Thereafter, either may call first with equal frequency. Not all calls are answered, but when they are, the response is rapid;

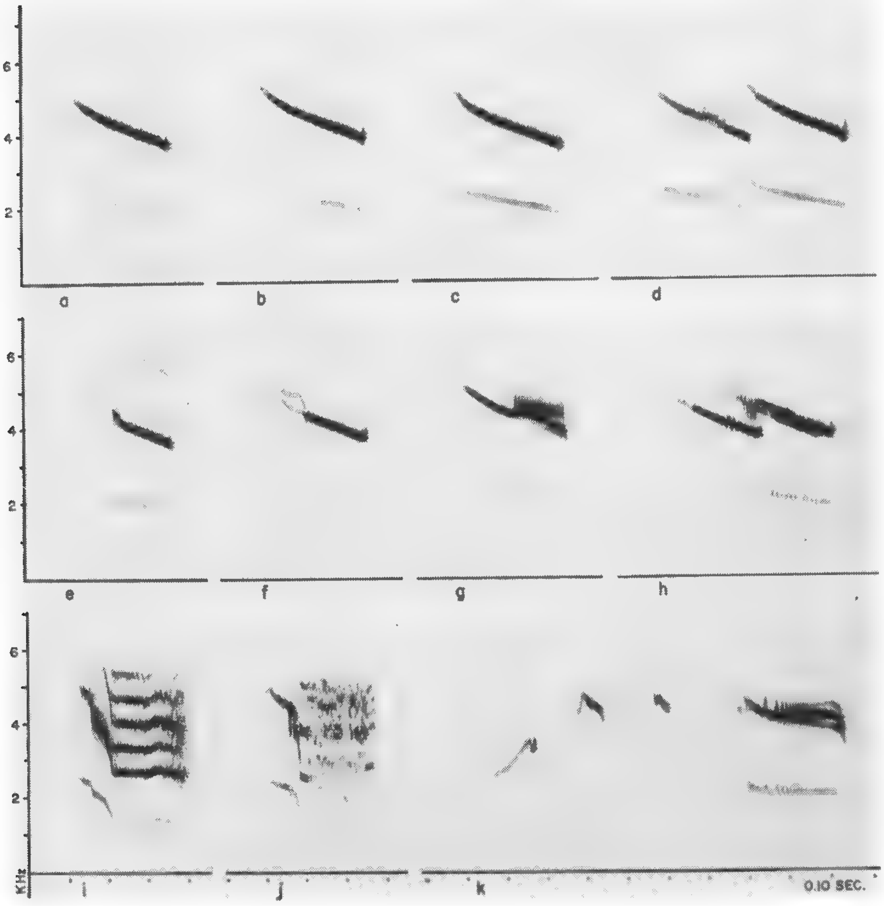


Figure 3. Sound spectrograms of vocalizations of the Wire-tailed Manakin. The call (*eeew*) is shown in its normal pattern; four different birds are represented (*a, b, c,* and the second sound-figure of *d*). Various forms of modulation of the call under stress conditions are shown (the first sound-figure of *d*, and *e* to *h*). Figures *d* and *h* show Answer-calls. "Aberrant" patterns toward the end of the most active part of the breeding season tend to replace the normal call but are used in the same context *(i, j)*. A multi-figure call, of undetermined function, is shown in *k*. Further explanation of the nature and functions of calls is given in the text.

most often the responding bird starts to call before the other's call is completed (Figure 3d and 3h).

When delivering its call—a nasal, slightly harsh, monosyllabic *eeew*—the bird points its bill upward 45 to 80 degrees, exposing the yellow throat which puffs out; the bill remains closed. The call is short, not much over a quarter of a second, and is downwardly inflected, the fundamental frequency descending from about 2.6 to 1.8 kHz. There is remarkable similarity in the normal call of different individuals (Figure 3a and 3c and the second bird of 3d).

In producing its call, the Wire-tailed Manakin uses two voices (presumably, one produced by the internal tympaniform membrane in each bronchus), which may increase the amount of information communicated by an otherwise very simple sound. The two voices begin simultaneously, or nearly so, and are tonally consonant. Greater or lesser excitement results in manipulation of one of the two voices, which may begin later than the other voice, be slowly or rapidly modulated in frequency, and/or deviate tonally, resulting in beating, which is acoustically equivalent to amplitude modulation. This dissonance increases the burriness or harshness of the call, a sign of "irritation." The situation was ambiguously competitive when the calls of Figure 3e and 3f were given; 3g and 3h are from strongly competitive situations.

Given in the same context as a normal call is another sound, weak and scratchy, as if the calling bird had a sore throat. Such calls were recorded from one bird and sonagrams show the pattern, at least with this one bird, to be quite distinct from the normal call and to vary in all degrees from acoustically organized to very unorganized (Figure 3i and 3j). In several display-area owners this aberrant call tended gradually to replace the normal one toward the end of the main nesting season. In one owner the vocal change occurred rather abruptly and thereafter all the bird's calls had this weak quality. We cannot offer a precise explanation. Not long after such calls develop, the manakins become inactive and they begin their annual molt. This suggests the possibility of hormonal influence on the call and, in turn, that vocal variations at times of stress may be under involuntary control.

Another vocalization, a multi-figure call (Figure 3k), is uttered rarely and usually only when an owner is alone; but in one case of birds competing for a display area it was given infrequently by both birds during periods of inactivity. The first sound-figure seen in the illustration is sometimes lacking and the last one is not always strongly modulated, but the consistency of basic pattern suggests that this vocalization has a meaning that has not become clear to us.

Whistles

More or less frequent in the Wire-tailed Manakin's vocal repertoire are whistled calls that vary in duration and sharpness (Figure 4). Plotted as a function of their length (Figure 5), 231 recorded whistles cluster into two

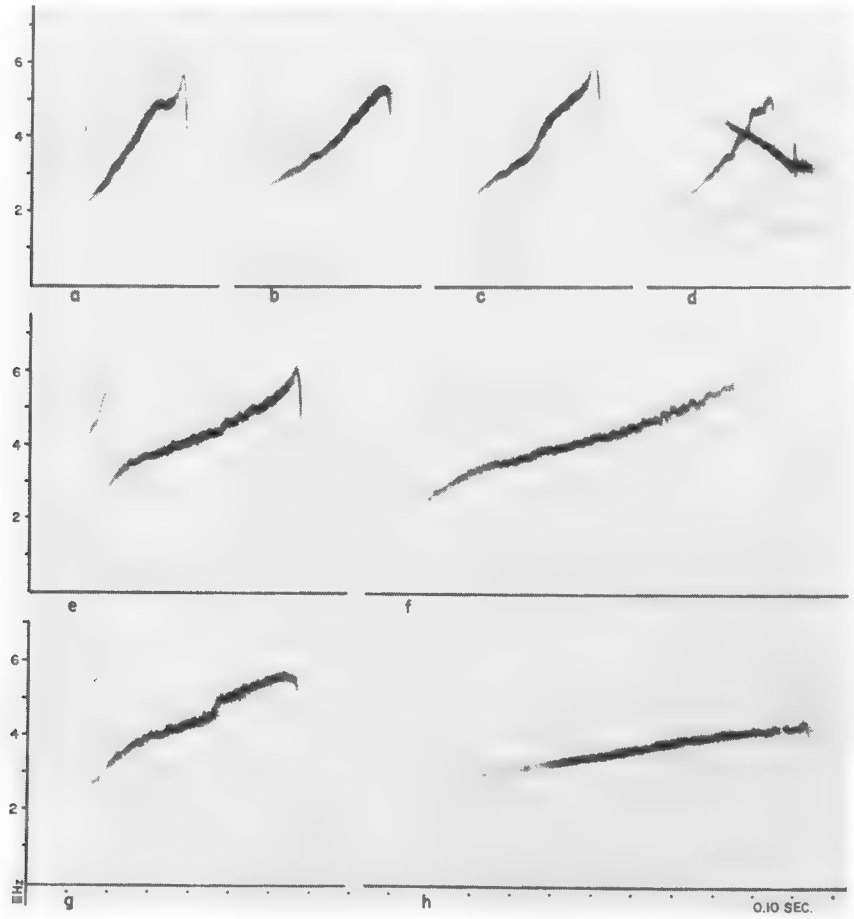


Figure 4. Sound spectrograms of whistles of the Wire-tailed Manakin. Conflict Whistles *(swee)* by four different birds (*a* to *d*; the other sound-figure in *d* is a Pass-by Call); Appeasement Whistles *(sweeee)* of different duration and pattern *(e* to *h)*. See text for explanation of nature and functions of whistles.

discrete groups: those of less than 0.4 seconds duration, and those of 0.5 seconds and longer. The former qualify as Conflict Whistles and the latter we denote as Appeasement Whistles. The clear dichotomy suggests that there has been selection favoring a separation of whistles of decidedly different nature. As the basic pattern is similar for all the whistles, the interval of 0.10–0.15 seconds between the two categories may serve to permit the birds to distinguish unmistakably between them.

Conflict Whistle: Sounding like *swee*, this is an essentially pure tone inflected rapidly upward, then sharply downward. Figure 4a to 4d shows the whistles of four different individuals; the observable variation represents equally well the variation in the patterns of a single individual. This whistle is delivered with the bill slightly open and not pointed upward, although the throat bulges.

The Conflict Whistle has been heard only during, or in relation to competition for ownership of a display area. It may be the most frequently uttered vocalization, but calls of both normal and variant pattern are also given occasionally (Figure 3d, 3g, and 3h) and may increase in proportion to Conflict Whistles if the contestants begin mutual displaying. This is a curious development. The Wire-tailed Manakin is one of the few species of this family in which two males perform coordinated displays as part of normal display behavior. The urge to display is apparently strong and so even competing birds sometimes display together, although not with the smooth coordination of a fully cooperating twosome; and they continue to emit conflict whistles while displaying together. Figure 4d shows an active partner giving a Pass-by Call and the passive partner on the display perch giving a Conflict Whistle as it ducked. With fully cooperating birds, the passive partner would, if it called at all, have given a normal call as in Figure 6d.

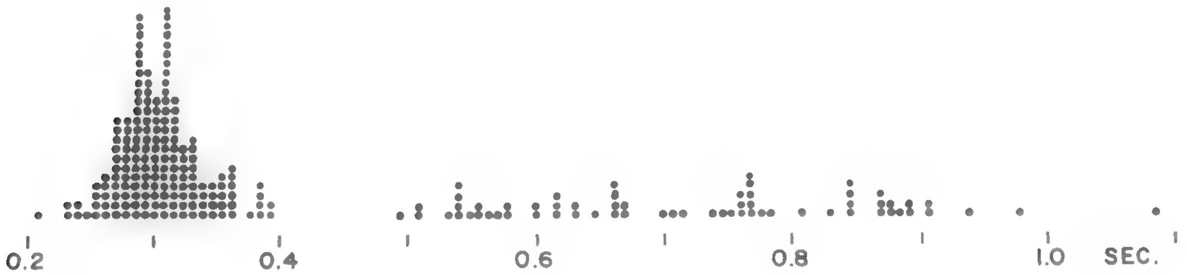


Figure 5. Whistles of the Wire-tailed Manakin, recorded from 1975 to 1978 in the main study area, plotted as a function of their duration. There is a clear separation into two categories: Conflict (<0.4 sec) and Appeasement (0.5 sec and longer). At least eight individuals are represented in the conflict category, at least six in the appeasement; at least five individuals are common to both categories. The different sample size in the two categories reflects the relative frequency with which Conflict and Appeasement Whistles are given in their respective contexts. Further explanation is given in the text.

Appeasement Whistle: As the term implies, the Appeasement Whistle is given by one bird to convey to another that it is not aggressively inclined; in some contexts it seems to serve as a vocal invitation by a display-area owner for a visitor to join it. It is pure-toned like the Conflict Whistle but is more quietly delivered and more prolonged *(sweeee)*, the pitch rising slowly rather than sharply and emphatically. Figure 4e to 4h illustrates short and long Appeasement Whistles of slightly different pattern.

The nuances of meaning within the great range of Appeasement Whistles are not completely clear. For females, an owner emits longer whistles. He uses both long and short whistles, but mostly the former, to reassure or invite a reluctant male display partner. The full range is employed by both members of a cooperating twosome. Some observations suggest the shorter type may represent ambivalence; ambiguous situations do arise and even between cooperating display partners there is apparently a latent sense of competition.

To extend these generalizations into the realm of the Conflict Whistle, in a context of incipient competition (i.e., where a formerly cooperating partner had begun to act as pretender to ownership) whistles of all kinds were heard. It was often not possible to tell which bird whistled, but when the identity could be established, the pretender gave mostly Conflict and an occasional short Appeasement Whistle, whereas the owner gave all types, but only rarely those of long appeasement. In contexts of outright competition, almost all whistles by both birds are of the conflict type.

The Klok

The Klok is a two-part sound, incisive but somewhat resonant, that can be imitated roughly by "clocking" the tongue. The first sound resonates at a higher frequency than the second (Figure 6h to 6k). It appears to be mechanical, probably produced by the wings, and is given most usually at the end of a flight, just as the bird is to land on a perch. Occasionally it comes a moment after the bird alights and then, if one is watching intently, a quick flick of the wings is seen. Its exact function is not clear, other than to serve as an attention attractor. In what appears to be a low intensity display, flights are made from perch to perch in a display area, each ending with a Klok. These flights are usually between perches two to six meters apart, occasionally as little as 60 cm, and frequently the trajectory dips downward until the bird is close to the perch and then rises at the last moment. Often the bird calls very shortly after alighting with a Klok. Kloks serve also to punctuate other displays.

Displays

Side-to-side Jumps (Side-jumps)

Oriented transversely across the perch, the bird jumps very rapidly to one side over a distance of eight to ten cm and at once back to its original position. The double movement takes a bit over a third of a second. When Side-jumps are repeated in series, as they often are, with a pause between them about as long as the completed jump, they are performed at a rate of about four in three seconds—the bird seems more like a mechanical toy than a living creature. The jumper's stance may be little different from typical perching but is usually modified by raising the bill slightly, depressing the scarlet crown and upper mantle, and partially fluffing the black feathers of the posterior dorsal region (Figure 7a and corresponding inset).

The jumps may be to the bird's left side with an occasional deviation to its right, or the inverse; they are not haphazardly right and left, although sometimes a left-center-right-center sequence occurs with no pause between the jumps. Similarly, the typical single jump to the side is occasionally replaced by two to four smaller jumps in one direction with a single return

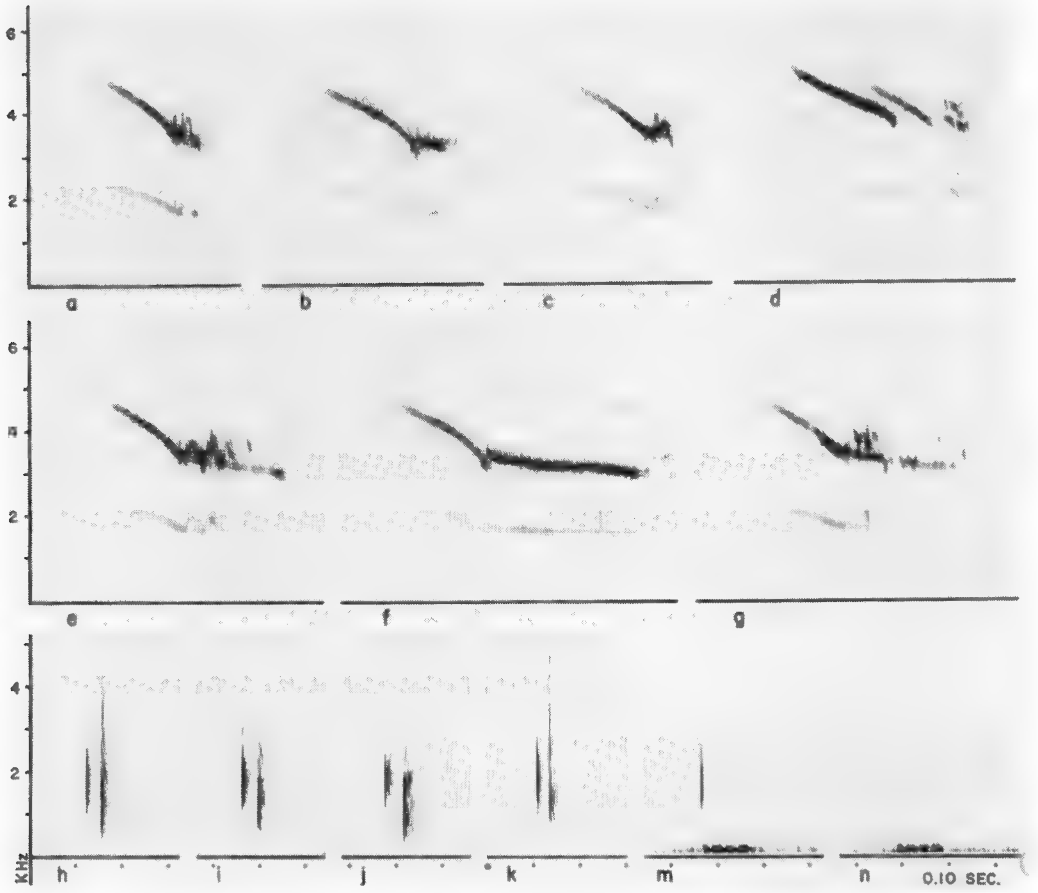


Figure 6. Sound spectrograms of vocalizations and mechanical sounds used in the Swoop-in Flight of the Wire-tailed Manakin. Pass-by Calls *(eeeo)* by four different birds: *a* to *d*; the first sound-figure in *d* is a Call *(eeew)* by the passive bird on the display perch. Culminating Calls *(eeeooo)* by three different birds: *e* to *g*; these were given by, respectively, the same birds that uttered Pass-by Calls *a* to *c*. The Klok recorded from four different birds: *h* to *k*. The Kloop and oop: *m* and *n*. The Klok is not limited to Swoop-in Flight context. Explanations in text.

jump. Some individuals show this variation more than others. In normal Side-jumps the wings are not quivered.

Side-jumps, often with interspersed calls, signal the jumper's position and invite another bird to join it there. The jumps are performed mostly on a display perch but also at times on an auxiliary perch from where the focus of activity is easily transferred to a main perch. Side-jumps seem seldom, if ever, to be given *in vacuo*. A bird alone that is Side-jumping has sensed, sometimes erroneously, the presence of another Wire-tailed Manakin.

Stationary Display

When a Wire-tailed Manakin is highly motivated to display and the partner, or presumed partner, is slow to join it on the display perch, the manakin changes from the typical Side-jump stance to a Stationary Display: the body is tilted forward, the head lowered and pointed forward, the tail raised to about horizontal, the back and rump feathers are raised and parted so that the bird has a strikingly spiky appearance in side view, and the wings are drooped, but not far enough to show the white (Figure 7b and 7c). In this position with the body usually obliquely angled to the perch, the bird vibrates its wings but remains otherwise essentially still. It may peer at the canopy where the object of its interest is known or presumed to be.

Although this Stationary Display may be held for some seconds, it is mainly transitory. In some contexts it seems to reflect ambivalent behavior. We categorize it because of its relation to, and effect on, some other displays. For example, if the partner still does not come to the perch, the displaying manakin may revert to Side-jumps, often remaining in the crouched stance, and these may be mostly the series of small jumps seldom used in normal Side-jumping (Figure 7b and 7c inset). Also, the displaying male may continue to quiver the wings, something it does not do in normal Side-jumping. At times, aligned more nearly with the perch, the bird performs multi-jumps in either direction, and forward or backward, for as much as 30 cm along the perch, instead of returning to the start with a single jump.

Butterfly Flight

In what appears to be a position somewhat similar to the posture for normal Side-jumps (Figure 7a), but with the dorsal feathers often more erect, the male flies with slow and shallow wing beats and the flight feathers spread, showing conspicuously the white patch in each wing. Butterfly Flights are made usually over distances of two to six meters. The flight path is horizontal or slightly ascending or descending. The displaying bird rarely calls during a Butterfly Flight and may or may not alight with a Klok.

While they serve as a component of more complex display sessions, Butterfly Flights are used also as a self-contained display, given when another bird is present, although the other bird does not necessarily have to be seen. For example, in reaction to the playing of recorded calls and Kloks in one display area, the owner flew to a perch near the sound source and

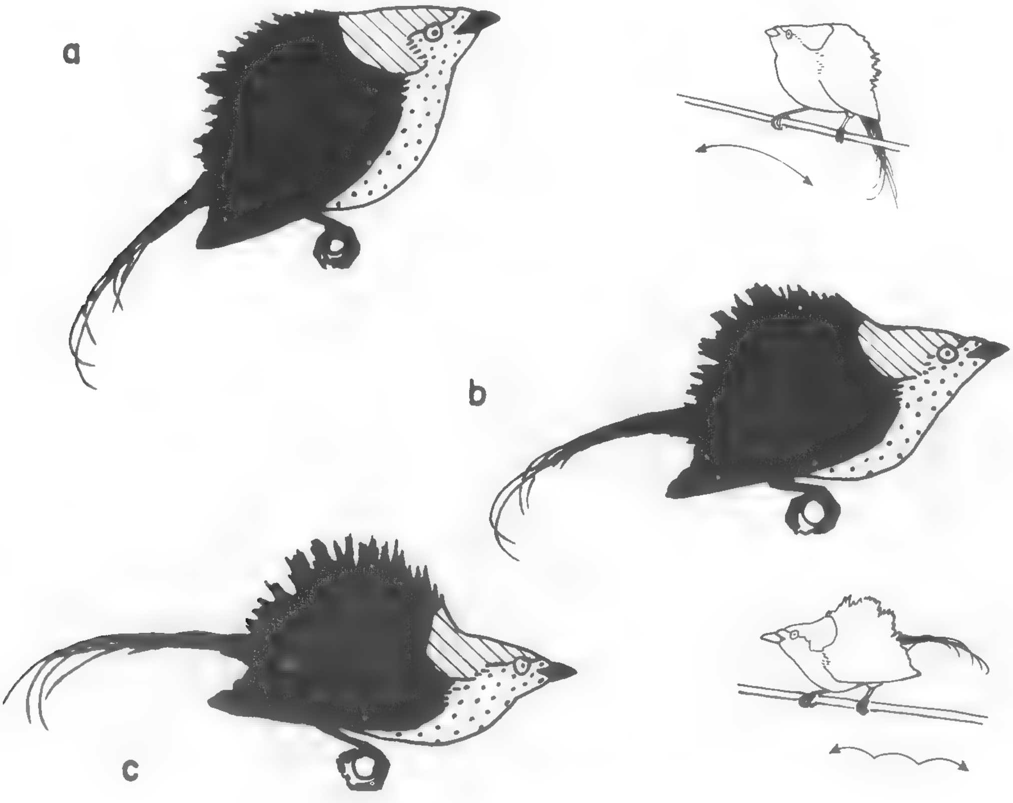


Figure 7. Postures of the Wire-tailed Manakin as used in Side-to-side Jumps *(a)* and Stationary display *(b* and *c)*. The insets represent *(above)* a typical Side-jump and *(below)* a Multi-step-side-jump.

began a long series of Klok flights away from that perch and back to it again. About half of these were Butterfly Flights, but only on the flights away from the perch.

The Twist

This is the name we gave to the display that answered the long-asked question: what is the function of the tail filaments? The answer astonished both of us. The filaments are not for visual display as had been thought; at least, not primarily. They are tactile organs of a quite unique kind: with them one bird brushes the other on the face or throat.

For its full realization the Twist requires two cooperating birds, one of them active, the other passive. Starting from a Stationary Display, which may be held only momentarily, the active bird further lowers its head, raises its tail, and with vibrating wings begins to pivot or twist its body fairly rapidly from side to side across the perch through an angle of about 60 degrees, sometimes more. It is oriented facing away from its partner. Slowly it hitches along the perch, with jerky backward movements, at the same time increasing the tempo of its twisting and raising its tail even more. The partner, who is perched normally, edges toward the active bird. When the birds approach closely enough there is physical contact: in its whipping back and forth, the twisting bird's tail brushes the partner rhythmically (Figure 8).

The twisting bird's exaggerated position places its down-curved tail filaments at face level of a typically perched partner, but the angle of the perch may vary this height. At its most rapid tempo, with one bird brushing another, the pivoting rate is 2 to 2.5 full cycles (to one side and back) per second. Young male partners sometimes bite at the tail, or at the twisting bird's crissum; but they eventually heighten their stance or raise their head so that the tail filaments brush the throat. Some younger birds lower their head instead of raising it. Partners who have learned may approach the active bird in an already appropriate upright stance.

The twisting bird alternates the position of its feet on the perch with each pivot. The feet are apparently held in position until the last moment, then snapped very rapidly to the new position. Rapid twisting provides the observer with the visual impression that the direction of the toes is reversed with each pivot while the tarsi remain in position, an optical illusion that misled us for some time until we were able to observe under optimum light conditions twisting birds with a different color band on each leg. At the slower rate and narrower angle of incipient twisting, however, a bird may not alternate its legs. One young male was seen to pivot with one foot in a fixed position, the other foot moving first to one side, then to the other, of the fixed foot. The included angle of this young bird's Twist, which seemed slower than normal and not of the best form, was considerably more than 60 degrees, perhaps double that.

Almost invariably, Twists are performed only on one of the main perches. In a well-coordinated display session, male partners alternate the active and passive roles. At times a bird interrupts the Twist with a call. Most such calls have a normal pattern but an occasional one shows some variation.

We have represented the Twist in its fundamental, fully realized form. It does not always develop so. The birds may not approach closely enough, so that the tail filaments fail to contact the passive partner. Sometimes both birds are eager to take the active role and incipient twisting by one bird is inhibited by similar behavior from the other, although we witnessed one instance where the partners ignored convention, and rears affront, brushed each other's tail. One of these birds was in early immature plumage and it is usually such birds that act aberrantly, probably from inexperience.

The Twist is often performed without a partner, as part of a display sequence executed *in vacuo*, or when a female or male in the vicinity has not yet come to the display perch. In such cases the twisting bird may at times move up to 30 cm along the perch and back again. In solo Twists there is, of course, no physical contact made by the tail filaments. But one display-area owner had acquired the unique practice of backing up to a twig projecting vertically near the proximal end of its display perch, and when an animate partner was not present the twig served as a regular substitute. There is no doubt about the voluntariness of this action or that physical contact was made with the twig. While this seems an unnatural behavior, it is curious that other males have not learned it. Half the main perches in our study area had equivalent vertical projections, but the only other incidents seen in many weeks of observation were of purely accidental occurrence. These display-area owners were under observation for several days before and after the accidental brushing and did not repeat. The owner who had learned the practice very probably did so by an accidental brushing against the vertical twig.

Swoop-in Flight

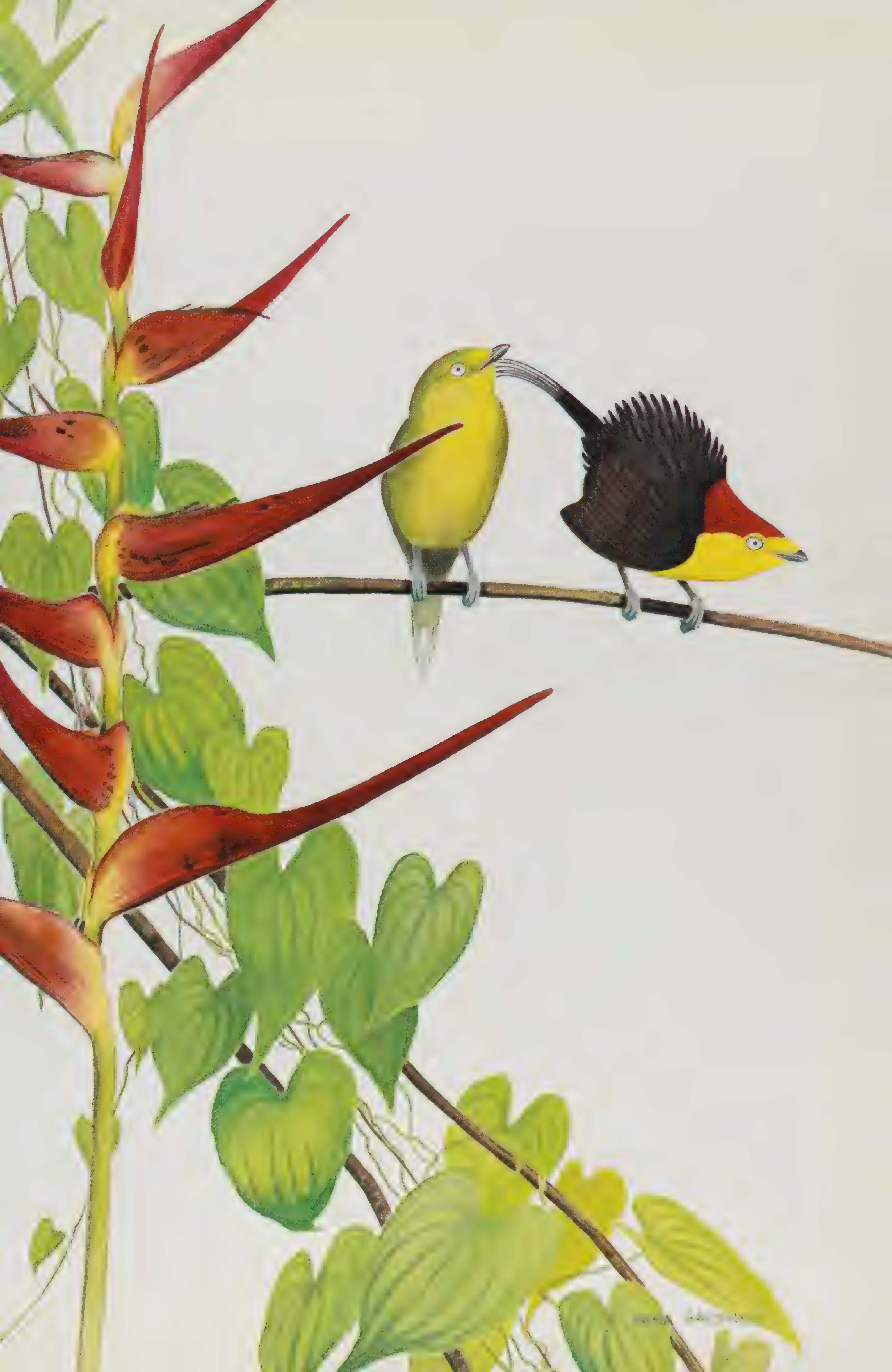
This highly ritualized flight is usually directed at a partner, male or female, on the display perch and involves coordination of one kind or another between the two birds, but it is often performed by one bird alone and that is how we introduce it.

The displaying bird flies rapidly outward or upward from the main perch for a distance of 10 to 15 meters, Kloks as it perches briefly or barely touches the far perch, then returns in rapid flight with a dipping trajectory, zooms over the main perch and, with another little dip, alights with a Klok on an auxiliary perch (Figure 9). The two Kloks are a usual but not invariable part of the flight. Another mechanical sound, a Kloop in the descending portion of the return flight, is also a very frequent feature. Almost invariably included is a Pass-by Call as the manakin zooms over the main perch.

The Kloop begins with the first part of a Klok and continues as a four-pulse low frequency sound; sometimes this beginning is omitted and the sound is only "*oop*" (Figure 6m and 6n). The Kloop is produced by the flying bird's wings. Each pulse of the sound corresponds apparently to a wing beat and at this time the white wing patches flash more conspicuously than in the rest of the flight. This probably explains why the Kloop is produced in the descending part of the flight; the flying bird is thus oriented better to show the white flashes to a bird on the display perch.

The Pass-by Call *(eeeo)* is patterned much like a normal call but with a strong modulation of the terminal part (6a to 6d). In the Swoop-in Flight, a male does not always continue to an auxiliary perch; sometimes he veers rapidly back to, or alights directly on, the display perch. In this case the Pass-by Call is prolonged to become the culminating call, *eeeooo* (Figure 6e to 6g). The basic consistency of the patterns of Pass-by and Culminating Calls has been confirmed by numerous sonagrams; intra-individual variation can be almost as great as the inter-individual variation illustrated.

Wire-tailed Manakin, *Pipra filicauda*. Painting by Dana Gardner.



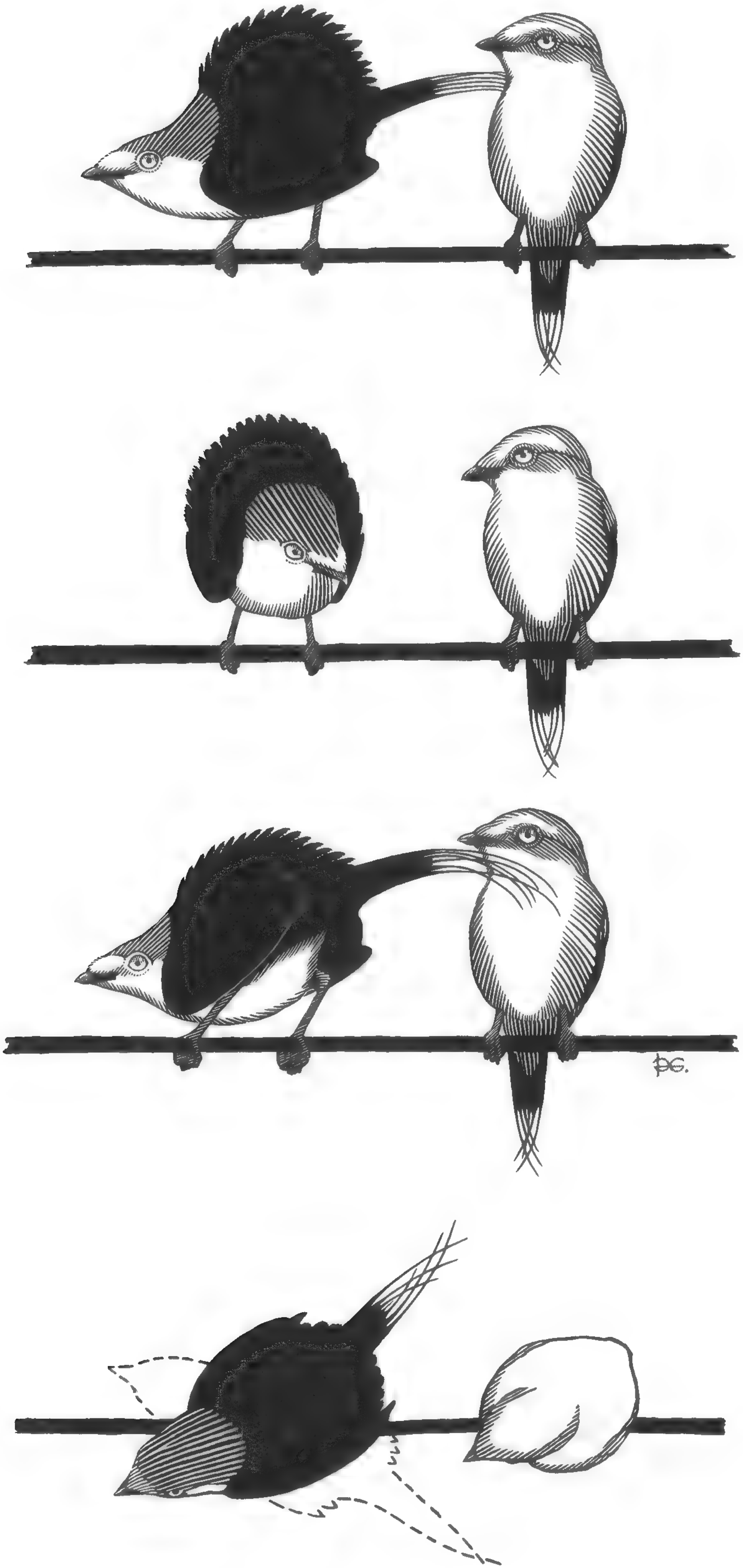


Figure 8. An adult male Wire-tailed Manakin performing the Twist display with a partner. Bottom drawing shows the positions of the birds viewed from above. Drawing by Dana Gardner.

On occasions when the displaying male loops back to the main perch he frequently performs the Flutter. Appearing to be falling backward, he flutters his wings and treads his feet; both the head and the posterior region are depressed. Or the bird may Flutter with the body high on outstretched legs, the toes gripping the perch. We have also observed Flutters performed suddenly by males loafing on perches, and one male was seen twice to fly to a perch a meter away and perform a Flutter and "copulation" on a small bracket fungus growing there; in these cases there was no call given. All these actions are apparently differently developed pseudo-copulations. Similar behavior has been observed in other *Pipra* species (Snow 1963b:557; Lill 1976:12).

The loop-back and Flutter occur with greater frequency when a male displays alone, which may mean only that his partner, although present, is momentarily inactive, or is trying to entice him to a different display perch in the display area. These behaviors may be performed by the owner or by the visitor.

A Swoop-in Flight is not invariably accompanied by a Pass-by Call. If the displaying bird veers back to the main perch he may give a Culminating Call upon alighting, with or without a Flutter. The pattern of this call is the same as a normal Culminating Call.

Coordination of Displays

Let us now put the pieces together. In their displays, most manakins—and the Wire-tailed is no exception—move and maneuver so rapidly that it is very difficult to observe accurately every detail. Furthermore, although highly ritualized, their displays can be confusingly varied for one reason or another. An account based on any single one of our numerous observation periods, while no doubt a reflection of what we saw and heard, would present a somewhat distorted picture. Frequent observation under diverse conditions, however, has made clear the fundamental display pattern. Solo displays, especially those *in vacuo*, give a clear picture of the basic sequence of the elements of the main display for there is no inappropriate action by a partner to inhibit or interrupt its development.

Display Between Two Males

With the arrival of a male visitor in a display area there is often some initial flying about with Kloks, and perhaps a few Butterfly Flights. Calls and Answer-calls are frequent. Sooner or later the owner (or sometimes the visitor in well acquainted twosomes) begins Side-jumps on a main perch. If the visitor is slow about joining him, the owner may change to Stationary Display in anticipation of ensuing events, thereby enhancing his invitation. With the visitor on the display perch, a display bout begins.

From Stationary Display the owner begins to Twist. One or both birds may edge closer for the brushing. With no advance warning, the twisting bird departs suddenly with a rapid turn of the body in a curving trajectory downward and away for a Swoop-in Flight. This abrupt Breakaway is usually accompanied by a loud beating, at times snapping, of the wings. We give the Breakaway separate category because it is not an invariable feature and it seems intended to introduce an element of surprise into the total performance. The passive partner remains on the perch facing in the direction of the flying bird; it may call, or utter an Appeasement Whistle, especially if the

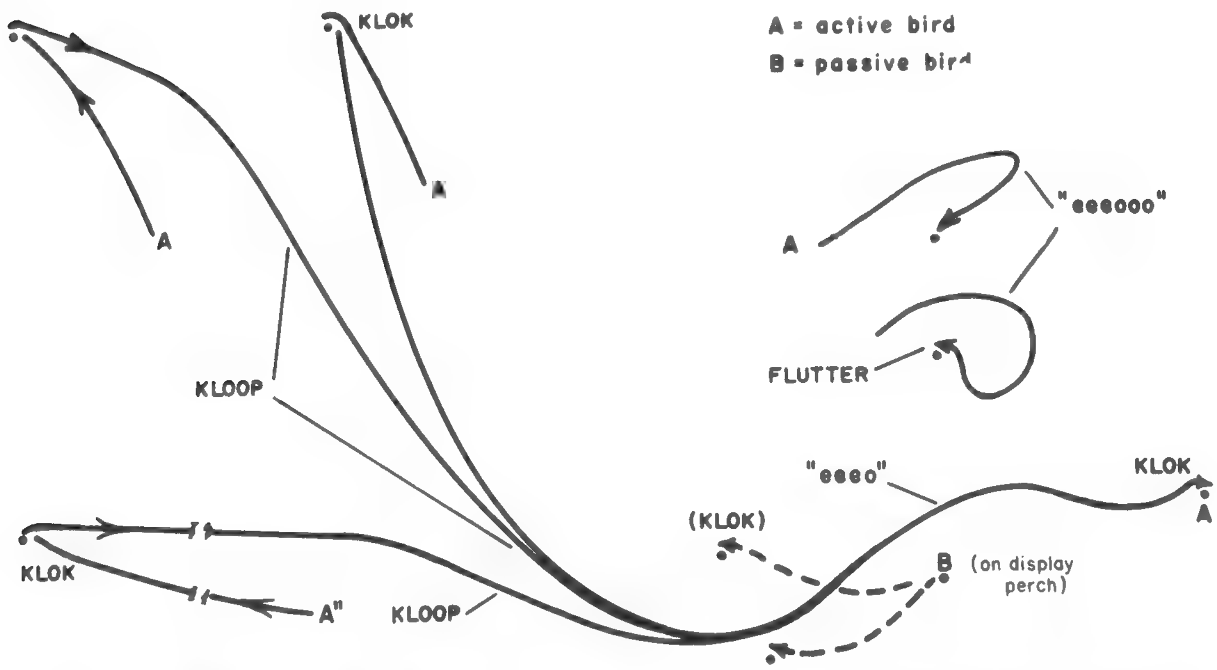


Figure 9. Diagrammatic portrayal of the Swoop-in Flight. One of the most important displays of the Wire-tailed Manakin, it is shown here as part of a coordinated display between two males (A and B). Several typical flight paths are indicated (A, A′, A″). The thin lines to the left of flight path A′ indicate the most usual range in the more vertical flight paths where the Kloop is produced. Dots represent perches. This display is directed toward the passive male (B) on the main display perch. The insets show the active male (A) veering back to the vacated main perch rather than continuing to an auxiliary perch as he does usually. Detailed description of the Swoop-in Flight is given in the text.

other bird delays a bit on the far perch. It also may call, sometimes by design, sometimes by coincidence, as its returning partner swoops toward it, in which case two calls are heard if they are temporally separable: the perched bird's *eeew* and the flying bird's *eeeo* (Figure 6d).

When the flying bird is but a moment away—the time from Kloop to pass-by is less than a second—the perched bird, whether it calls or not, usually flits to an auxiliary perch, sometimes alighting with a Klok. If it should remain on the main perch—sometimes especially likely to occur in a competitive situation—it often ducks as the other passes close over its head. But whether the passive male leaves the perch or not, the active bird usually continues beyond as described earlier. At times it may alight on the vacated perch or veer suddenly back to it. It may even alight on the perch with its partner still in place. These cases are proportionately few.

The usual situation at the end of a Swoop-in Flight is that both partners are on auxiliary perches. Both return to the display perch to begin the next sequence. The bird that was in the passive role will now become the active partner, and most often it returns first; indeed, in its flight from the display perch, it may barely touch the auxiliary perch and flit right back, often with a Klok on one or both landings. If its partner delays a bit, it performs Side-jumps and/or Stationary displays. The formerly active bird returns, often with a Butterfly Flight, and becomes the passive partner. The now active partner performs the Twist, Breakaway, and Swoop-in Flight. This sequence repeats itself time and again, three and even four times a minute. Such display bouts usually last a minute or two but may continue for five or ten. Sometimes several bouts succeed each other with only a few minutes intervening, forming display sessions of up to 15 or 20 minutes.

One experienced twosome, that could be observed well from sufficient distance not to inhibit the birds' behavior, was most impressive in its performance, not only for the duration of its bouts and sessions but also for the birds' awareness of their alternating roles. Their main perch was slightly inclined. On such a perch, it is advantageous for the active bird to be uphill from its partner. If the passive bird remained on the perch, after its partner's pass-by it moved uphill to be ready to play the active role. If it had left the perch, as it usually did, it returned to an uphill position; but if it chanced to return to a lower position, or if its partner came back uphill from it, it hopped over the partner to take its proper turn. Some statistics can be extracted from our recorded notes, made when we were able to coordinate our reflexes with the rapid action of the birds. Of 43 sequences, only two missed in the alternation of roles. In eight sequences, the passive bird remained on the main perch; this was always the display-area owner. In two sequences, the active bird, both times the visitor, veered back to the vacated perch. In only 19 of the remaining 33 sequences when the passive partner left the main perch was it clearly noted which bird returned first; in 16, it was the passive bird (10 of 11 in one bout). The display sequences followed each other in quick succession: in short bouts (1 to 2 minutes) at 10- to 16-second intervals; in long bouts at 10- to 40-second intervals. Over 75 percent of the intervals (from the start of one display sequence to the start of the next) fell in the 10- to 23-second range.

Many displaying twosomes perform according to the basic pattern for short periods, but many other times the display sequences are intermittent with no regular rhythm. A bout may abort after it barely has begun. The visiting partner in the most smoothly flowing coordinated displays is usually a male in advanced immature, but less than definitive adult plumage. Such a bird apparently still is subordinate in the hierarchy but is well experienced in display routine. Nonetheless, the smoothest performance comes only after some mutual experience between the two birds. Display bouts between males in adult plumage can be impressive but not quite so perfect. Perhaps the visitor's development confers on him essentially equal social status and inhibits the subtle subordination that may be required for optimum performance.

Even between well-acquainted partners there are deviations in the display routine. One such is a Swoop-in Flight performed when neither bird is on a main perch nor even on the same perch. This seems one way of renewing a display session that has lapsed. One bird directs a Swoop-in Flight at the other and continues on to a main perch. Deviations and aberrations are too numerous to recount fully. Two display bouts observed between an adult and a new partner, a young bird in early immature plumage, consisted largely of deviations from the basic ritual, and were remarkable because of the duration of such anarchic behavior, almost 10 minutes each time. The birds departed frequently on Swoop-in Flights without even a token Twist or, most unusual, when being brushed by the twisting partner. Similarly, when being brushed, a bird would flit to an auxiliary perch and back. Both birds bit at each other's tail. This is not exceptional for a young bird but it is unusual for adults. Swoop-in Flights terminated frequently with a direct landing on the display perch with the partner still there. There was no pattern to the exchanging of active-passive roles. The adult made most of the Swoop-in Flights, and with almost frenzied frequency. The intervals were shorter on the average than with even well coordinated partners displaying most actively, probably because of the elimination of the Twist from most sequences.

Male Behavior with Females

As true of all manakins that have been studied, the Wire-tailed Manakin shows a sharp division between the roles of the sexes. There is no lasting pair formation and the females alone perform the nesting functions and raise the young. The male's display area serves as a place where females come to have their eggs fertilized. Females do not always visit so directly. They may pass haphazardly into or through a display area in their foraging for invertebrate food. Their behavior is quite different from that of males, who come primarily to join the owner in display. Display-area owners, therefore, react instinctively to any movement in the canopy or shrub foliage. This leads to some mistakes, for the moving foliage may be the result of foraging birds of a different feather. Several birds in our main study area, for example the Sepia-crowned Flycatcher *(Leptopogon amaurocephalus)* and the Golden-fronted Greenlet *(Hylophilus aurantiifrons)*, frequently provide false stimulation for the male manakin. Even the movement of the foliage at the beginning of a light rain may send him into a flurry of display activity.

In general observations one cannot always be certain he is seeing a female Wire-tailed Manakin and not a young male. In a display area, however, females show no sign of performing the display activities of males, nor do they call. Young males call and engage in some display, no matter how inexpert. We clarify here that the birds we call female are either known to be such or have shown the combination of behavior and plumage that identifies them as females beyond much doubt.

The male manakin does not pursue the female, even when she is in sight. He tries to attract and reassure her, and eventually entice her to a display perch. He calls and flits from perch to perch, occasionally with Klok flights but mostly with Butterfly Flights. Our observations indicate that the Butterfly Flight is used much more frequently when displaying to females than to other males. Side-jumps on a main perch are a prime signal of invitation for females as well as males. If the female shows no interest or seems hesitant, Appeasement Whistles convey the male's pacific status or enhance his invitation. Further delay may inspire him to Stationary Display and more Side-jumps, even to solo display sequences. Constantly he peers at the spot where the female is, or he thinks she is.

Whenever we have managed to see the female who inspired such courting, she has left without going to the main perch (at times our presence may have inhibited her). The male sometimes flew after her but usually stopped at the edge of his display area. With Appeasement Whistles, he tried to win her back. It is interesting that those females seen to go to a main perch did so with little or no prior display activity directed to them by the owner. This proved true at all times of the year. Nonetheless, it may be that the male's performance is effective in alluring young females, serving to make known to them the location of the display area and the position of the main perch, and acquainting them with potential mating partners.

When an experienced female Wire-tailed Manakin alights on the display perch, the male begins to Twist. He may hitch backward toward her, but that is unnecessary for the female loses no time in sidling toward him. Here we must distinguish between two behavior sequences. In the first, and generally the more impressive, the twisting male Twists for 10 to 20 or more seconds. He pauses a moment, just long enough for a call, and Twists again and again. Then he freezes abruptly on the far half-cycle of a pivot and in the extreme Twist position, with head low, tail high, and body motionless except for the drooped vibrating wings, his posterior is exhibited to the female (Figure 10). After some seconds of holding this position, he renews his Twisting. Then a Breakaway flight with a snap of the wings, and a Swoop-in Flight. With his returning Kloop, the female ducks off the perch. The male zooms over with a Pass-by Call and lands beyond, then returns to the perch in Butterfly Flight. If the female has not yet returned, the male Side-jumps. The female does not tarry; sometimes she is back first, but she does not Side-jump. The male renews his Twisting. And so on. This activity continues for many minutes, even up to ten or more—ten minutes devoted mostly to the Twist, punctuated by some calls, some Tail-up-freeze display, and an occasional Swoop-in Flight. During the male's Twisting, the female is looking obliquely toward the male and is being brushed by his tail two to three hundred times a minute.

Three such performances, two in one display area and one in another, were observed during a five-day period in late November. This is well outside the main nesting period. During the peak nesting period, roughly mid-April to mid-July in our primary study area, the only visits by females to main perches that we saw were relatively brief. In fact, the only two that terminated in copulation were reduced to what may be the minimum essential ritual. In one of these, seen in splendid detail, the first indication that a female might have arrived was that the display-area owner, inactive on a sub-canopy perch, suddenly assumed the Stationary Display stance and performed some agitated multi-step-side-jumps, peering constantly at a place in the lower canopy. He then made a long Butterfly Flight on a descending course to an understory perch. The female followed, but stopped on a perch about half way toward the male and a moment later flew toward the main perch, alighting on the vertical stem of the sapling from which it grew. The male flew at once to the main perch where he performed briefly some Side-jumps, the Stationary Display, and a Tail-up-freeze. The female hopped onto the perch; the male began to Twist and the female sidled close for

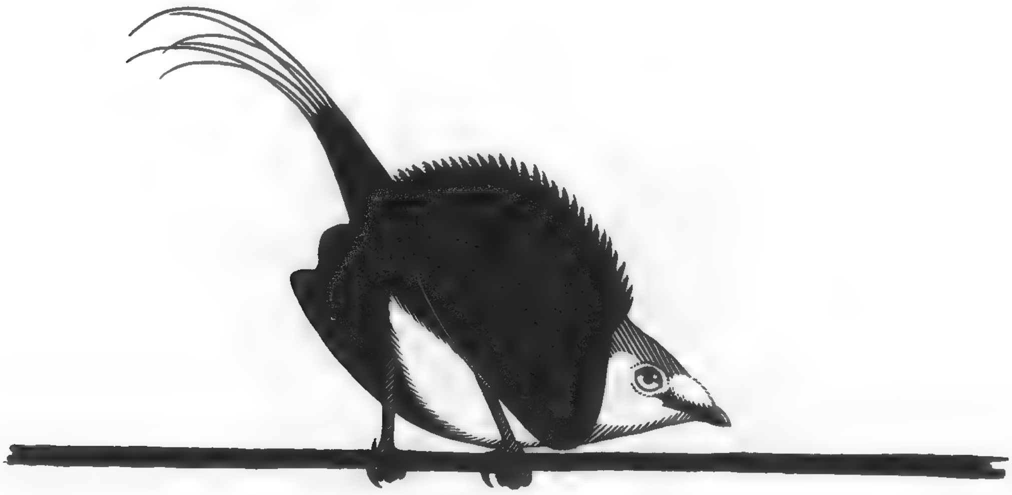


Figure 10. An adult male Wire-tailed Manakin performing a Tail-up-freeze for a female. Drawing by Dana Gardner.

the brushing. After Twisting for about ten seconds, interrupted once for a call, the male took off on a Swoop-in Flight. He had barely departed when the female assumed a pre-copulatory position with body slightly lowered and inclined slightly upward posteriorly. The returning male looped back with a Culminating Call, alighted momentarily beside the female, then hopped onto her back, fluttering there for a second or two before both birds maneuvered to effect cloacal contact. After coitus the male hopped to the perch, performed Stationary Display and a Tail-up-freeze. The female departed, but the male continued displaying for some minutes with Side-jumps, Klok flights, and frequent calls. Less than three minutes had passed from the arrival of the female in the canopy to the actual copulation. The other copulatory visit, involving other birds in a display area 300 meters away, was brief and similarly performed, differing only in minor detail.

In the male's Tail-up-freeze posture (Figure 10) the female sees a conspicuous area of yellow, crowned by black, and bordered on each side by white framed in black. The white patches of the wings are not visible in side view, except at times as a small, indistinct blur. It is the broad inner webs of the flight feathers that are white. With the wing drooped, these form a white area when the underside of the wing is seen—the female's point of view. The delicate tail filaments, although seemingly inappropriate for a conventional visual display, may be a further visual stimulus when their down-curved forms are held motionless only a few centimeters before the female's eyes.

When males give the Twist to other males, the angle of the pivot is usually about 60 degrees, perhaps 20 degrees to the rear of the perch and 40 degrees to the front; sometimes the angle is greater. A series of photographs of a male Twisting to a female shows unmistakably that, at least in this case, the angle of pivot was more like 110 degrees, the angle to the front being almost 90 degrees. This places the male broadside to the onlooking female so that she sees to good advantage the scarlet crown and mantle, the yellow face, and the white eye (the iris is more closed during display than in normal perching), set off against the black of the wings and fluffed-up back.

In total, the twisting male presents the female with a dazzling alternation of color patterns, enhanced by rustling wings and brushing tail.

Miscellaneous Behavior of Females

Within a display area, we at no time saw a female display, or engage in what we might interpret as incipient display, and the few times we were close enough during a display to hear even soft sounds, we noticed none by a female. On one occasion we were installed too close to the most favored perch in a display area. The owner and a visiting male arrived on the perch but, wary of our presence, transferred their display focus to a perch at the opposite end of the display area. They had barely left the main perch near us when a female alighted there and, after a brief wait, emitted a soft, modulated whistle. Fourteen seconds later she whistled again, more sharply; after a briefer pause she gave a similar whistle, and then one sharper than the previous two (Figure 11d to 11f). The female's whistled sequence seems to reflect increasing solicitation. The males heard the female and flew to our end of the display area, where they performed many Butterfly Flights; but they would not go to the display perch, and the female left. The males returned to the far-end perch and resumed their displaying.

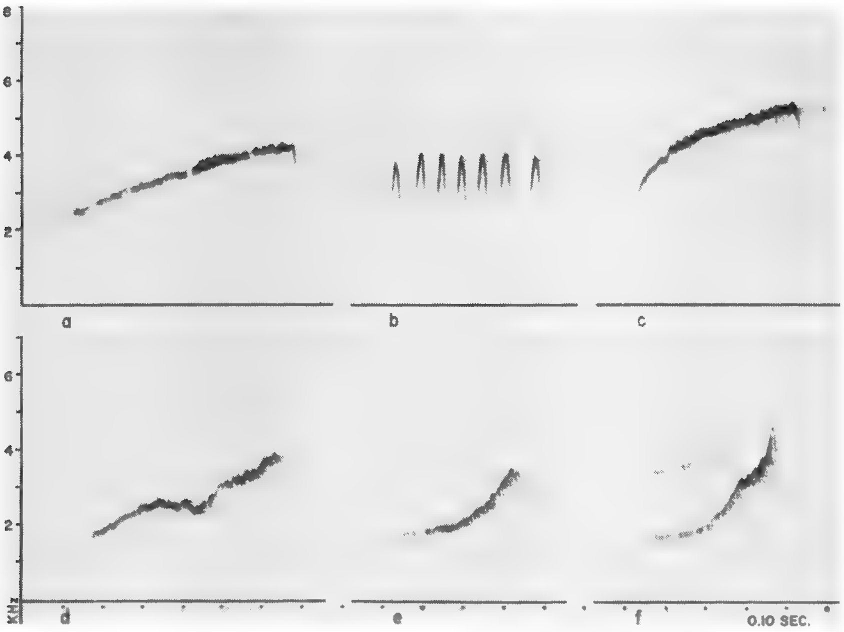


Figure 11. Sound spectrograms of vocalizations of female and young Wire-tailed Manakins. *a*. An appeasement-type whistle emitted by a female attending young recently out of the nest; *b*. A typical chatter phrase, the usual vocal communication of the female for fledged but still dependent young; *c*. The location call of fledged, dependent young; *d* to *f*. Whistles by a female alone on a display perch, apparently soliciting the attention of the male owner of the display area. The whistles portrayed are the first, second, and fourth of a series emitted by the female. They appear to reflect increasing solicitation because of the male's delay in responding. This was an unusual situation which is recounted in the text under Miscellaneous Behavior of Females.

Nesting

It has not been one of our objectives to make a thorough nesting study of the Wire-tailed Manakin, but we looked for nests as evidence relating to other behavior. Females show some tendency to build their nests amidst the foliage overhanging or bordering streams (Figure 12). Although frequently permitting close approach, they depart with no calls or other alarm sounds. One female brooding newly hatched young dropped to the ground and briefly performed a distraction display, fluttering weakly to low twigs and falling off as if unable to maintain her balance. When her young were older she gave no distraction display; but neither would she approach the nest when we were as far away as fifteen meters. On the other hand, females with eggs returned to the nest when we were no more than eight meters away.

When 13-day-old young were removed from the nest for color banding, they emitted at first a scratchy whistle. To this the female replied from the canopy with an Appeasement Whistle, and she continued to give similar whistles until we departed. Although females perform no displays in display areas, when we came upon one with young less than a day out of the nest, she made short flits terminating in half-Kloks (the first part of a normal Klok), apparently as a distraction. She also emitted some Appeasement Whistles (Figure 11a).

The location calls of fledged but dependent young are whistles that, although shorter than the Appeasement Whistles of adults, achieve the appeasement quality by virtue of the lesser upward inflection (Figure 11c). Females attending such young occasionally emit Appeasement Whistles, but the most usual vocal communication, both in close contact and when trying to locate young that have strayed from a previous position, is a chattery phrase of six to eight figures (Figure 11b).

Although it may invert the sense of evolutionary order of these whistles, it is probably advantageous for young and females, who wander frequently into display areas, to use Appeasement Whistles. Display-area owners may reply with Appeasement Whistles and occasionally we saw a male go to young whistling in the canopy, but generally young and attending females are ignored. The owners do not waste energy displaying for birds who will not respond. The whistles these birds give may be the signal that determines the owner's behavior. It may be noteworthy that the duration of the juvenile whistles falls in between the Conflict and Appeasement Whistles of adults. However, our sample of five sonagrams is too small to determine the validity of that finding.

Comparisons within the Superspecies Complex

Most of the elements of the display of the Wire-tailed Manakin are similar to elements of the displays of other *Pipra* species (for reviews, see Snow 1963b; Sick 1967a). These include (1) the dipping display flight (Swoop-in Flight) to the main perch; (2) an audibly or visually conspicuous landing on the display perch; (3) Side-to-side Jumps sometimes described as slides (in some species the jumps are so short and quick that the bird appears to slide); and (4) the backward movement (also described as sliding) toward

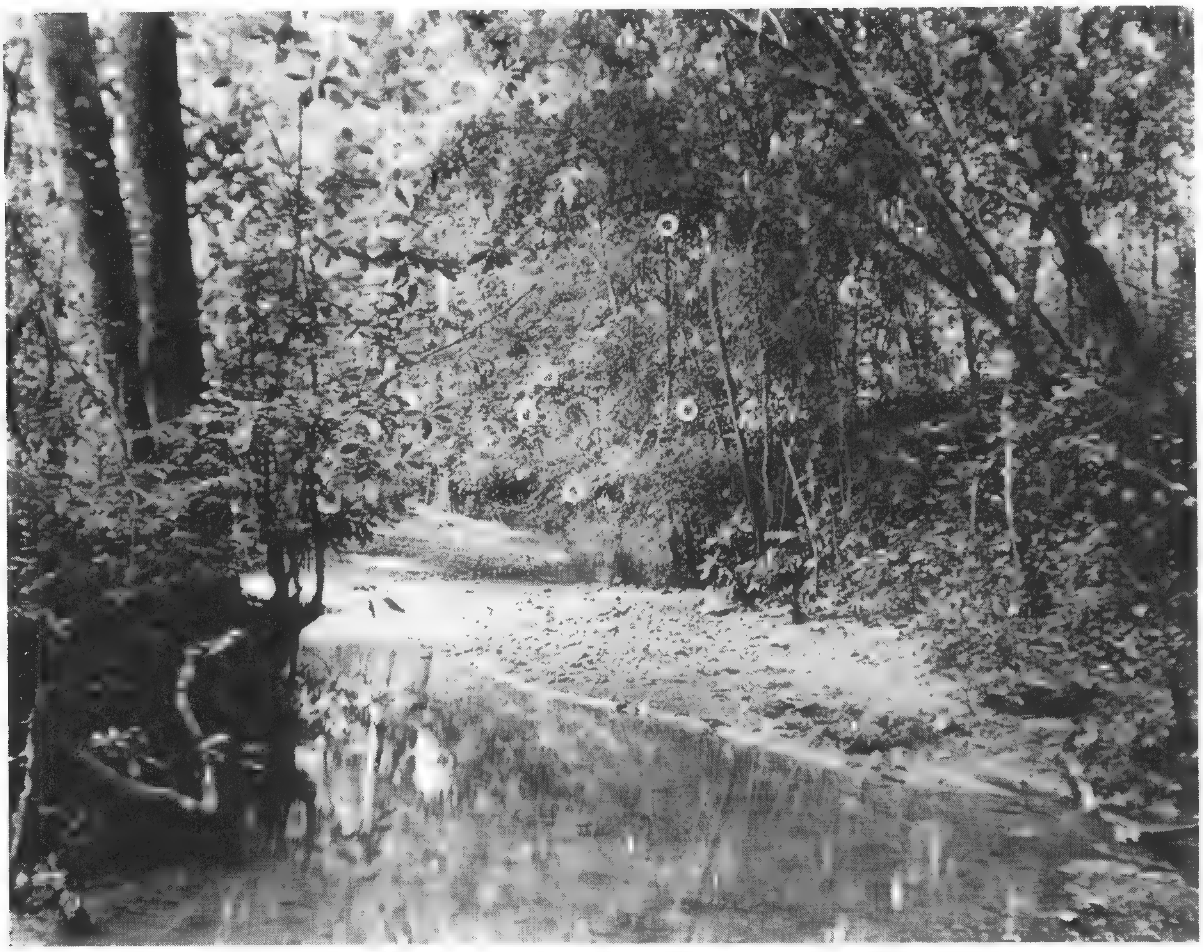


Figure 12. Female Wire-tailed Manakins show a strong tendency to build their nests amidst the foliage overhanging or bordering streams such as this one that flows through the main study area. Nests were found at different times in the places indicated by the circles.

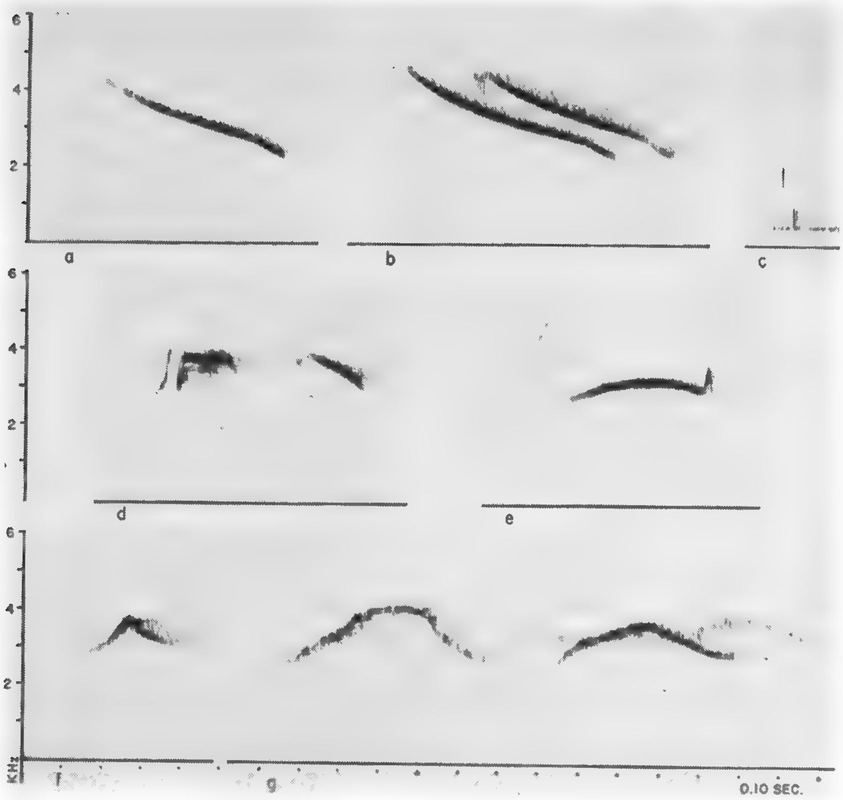


Figure 13. Sound spectrograms of recordings of the Band-tailed Manakin made near Manu, Peru by J. S. Weske *(b, c, e, f)* and C. Janson *(a, d, g)*. The Call and Answer-call *(a, b)* and the Klok *(c)* are obvious homologues of sounds of the Wire-tailed Manakin. The other vocalizations, mostly whistles, cannot be interpreted for lack of information.

the bird at which the display is directed. All kinds of variations are played on these main themes by the various species.

It would be desirable to make a full comparison with the two other members of the superspecies, the Crimson-hooded and the Band-tailed Manakins, but this is not possible, for the accounts of those species are based on only limited observations. However, a few similarities are evident that appear to be greater among members of this superspecies than with species of the genus *Pipra* outside this superspecies; and there is one major difference.

John S. Weske and Charles Janson kindly provided recordings of the Band-tailed Manakin, made near Manu in Amazonian Peru. Its call is very similar to that of the Wire-tailed Manakin but almost twice as long and roughly half an octave lower in pitch; answer calls occur (Figure 13a and 13b). No other vocalizations on the Weske and Janson tapes are similar in pattern to those of the Wire-tailed Manakin. They are mainly whistles and probably there are homologies but, lacking behavior notes, we can not determine these. Snow (1963a:45) described the advertising call of the Crimson-hooded Manakin as a "plaintive, somewhat drawn-out *eeeeew*." This seems to resemble more the longer call of the Band-tailed Manakin than the shorter call of the Wire-tailed Manakin. Sick (1967b:499) considered the voices of the Band-tailed and Crimson-hooded Manakins to be very similar.

Both of these species make a mechanical sound on landing which the published descriptions indicate must be like the Klok of the Wire-tailed Manakin. Figure 13c shows the Klok of the Band-tailed Manakin to be, in fact, very similar, but with the second part resonated at a lower pitch in this one example. Both allied species produce the Kloop, or its homologue, in display flights that are apparently very similar to the Swoop-in Flight of the Wire-tailed Manakin. In the Crimson-hooded Manakin, two cooperating males probably alternate roles in such display flights (Snow 1963a), which suggests a social organization between males similar to that of the Wire-tailed Manakin. The Butterfly Flight seems to be the same in the Wire-tailed and Crimson-hooded Manakins but is not yet reported for the Band-tailed Manakin.

Not surprisingly, the Twist, the effectiveness of which depends on the tail filaments, does not occur in the Crimson-hooded Manakin and is not mentioned by Sick for the Band-tailed Manakin. These species are apparently limited, in similar context, to displays that are essentially the same as the Tail-up-freeze and the Stationary Display phase of the Twist.

Evolution of the Twist and the Tail Filaments

The only important respect in which the display of the Wire-tailed Manakin differs from those of the Crimson-hooded and Band-tailed Manakins is in the addition of an entirely new element, the Twist, which brings into play the tail filaments. There is no mention of a pivoting display in the accounts of the other two species. Rapid and repeated about-facing is a feature of the display of the Red-capped, Golden-headed, Red-headed, and White-crowned Manakins (respectively, *Pipra mentalis, P. erythrocephala, P. rubrocapilla*, and *P. pipra)*. That it appears to be lacking in the Crimson-hooded and Band-tailed Manakins' displays seems odd, especially as the Wire-tailed's Twist may have derived from about-facing. Skutch (1949:6) describes the about-facing of the Red-capped Manakin as a pivoting about one leg. We observed a young male Wire-tailed Manakin in a similar motion. The modifications to about-facing that characterize the Twist probably developed slowly with the gradual evolution of this pivoting movement.

The Wire-tailed Manakin's tail filaments seem to be unique among tail feathers in birds in that they serve primarily, or entirely, as tactile display structures. Elongated tail feathers in other birds, when they have a function in display, are used for visual effect. The comparatively rapid evolution of a display structure and of the appropriate behavior that makes it effective raises the question of how such a behavior may have evolved. In this case the following considerations are relevant. First, elongated tail feathers occur in other manakins *(Chiroxiphia, Ilicura)*. In the genus *Chiroxiphia*, this character is developed to varying degrees in three species and is absent in one. It does not have an essential function in the displays, which are almost identical in the four species, except probably as a visual enhancement to the display movements. Among manakins, it seems that there is some predisposition for elongation of tail feathers. Second, on the assumption that the evolutionary development of the tail filaments in the Wire-tailed Manakin was gradual, in the early stages they were almost surely not employed regularly to brush the displaying bird's partner. However, with male and female close together on the display perch, accidental contact of slightly elongated feathers during about-facing may have proved unusually stimulating to one or both birds, either directly or by obliging attention to the visual display or otherwise enhancing it. It may be relevant that Skutch (1949:8) found that the male Red-capped Manakin sometimes "shook his tail rapidly from side to side" as he slid backward toward the female. The result of accidental tail-brushing was selection (1) for ever longer tail feathers, (2) for their downward curvature to place the ends in position for contact when the male's rear was elevated, (3) for their refinement to delicate structures that serve as brushes rather than clubs, and (4) for the modification of about-facing and tail-shaking to make the brushing of a partner even more effective. Thus, slight structural modification probably came first; but the tail as now found in the Wire-tailed Manakin and the Twist almost certainly evolved in concert.

The Twist display is obviously of primary importance to the male-female but not the male-male relationship. The long out-of-season (November) male-female display sessions observed, during which females are probably establishing or renewing relationships with future mating partners, are devoted mostly to the Twist. In the two matings observed, a Twist was part of the single display sequence that preceded the copulation. The positive way that females sidle toward males for the brushing also appears significant. Twists between males, on the other hand, seldom exceed ten seconds; most last only a few seconds. Frequently they involve only a token two to four pivots. In all these male-male displays, there is often no attempt by either bird to achieve contact for the brushing. At times the Twist is eliminated completely.

It is not unreasonable to think that the evolution of a plumage character so pronouncedly different from very close relatives may have been rapid. With the socio-reproductive system of manakins, sexual selection can operate with less restraint, and the way is open for the evolution of exaggerated display movements and the accompanying specializations of plumage and structure; for those males that most effectively stimulate females to mate with them should leave the most descendants.

Summary

The peculiarly modified tail of the Wire-tailed Manakin, *Pipra filicauda*, was for a long time believed reason for placing it in a monotypic genus, *Teleonema*, and was thought probably to have a visual function in the species' display, previously unknown. In this article we describe the display and some related behavior, based on observations over a three-year period.

The Wire-tailed Manakin's display behavior centers around non-contiguous display areas that vary in size from 200 to 800 square meters. Each display area is owned by a single adult male, who may perform alone or with a partner. The Wire-tailed Manakin is one of the few manakins in which two males perform coordinated displays. The visiting partner may be of any age class, except juvenile.

The display repertoire comprises elements such as Side-to-side Jumps, stylized stances, and short flights, with visually or acoustically conspicuous features which may be employed separately but are also used as part of integrated major display sessions. The two most important displays employed in such sessions are the Twist and the ritualized Swoop-in Flight. When male partners cooperate in the integrated display sessions, they alternate the active and passive roles; mutual experience improves their coordination.

The vocal repertoire of males includes a short call used for advertisement and contact; two modified calls used only in the Swoop-in Flight; and whistles that, although of similar basic pattern, separate into two discrete

categories based on their duration: one category of conflictive nature, the other not. Two mechanical sounds, the Klok and the Kloop, are employed in the displays and apparently are made by the wings.

Most of the elements of display of the Wire-tailed Manakin are similar to the elements of the displays of other *Pipra* species, especially to those of the Crimson-hooded and the Band-tailed Manakins *(P. aureola* and *P. fasciicauda)*. This would seem to confirm the suggestion (Haffer 1970) that these three species, which are rather similar morphologically except for the tail and are parapatrically distributed, constitute a superspecies.

In one display element, however, the Wire-tailed Manakin differs from all other manakins. This is a rapid pivoting action, the Twist, the function of which is to bring into play the bird's uniquely modified tail. The tail is not used for visual effect, as had been supposed, but is a tactile structure; with it the rapidly twisting bird brushes his partner on the throat four or five times a second.

Most visits by females to main display perches are made with little or no prior display inducement by the male. And female behavior is passive except for a determined sidling toward the twisting male to receive the brushing of his tail. Prolonged male-female display periods, with most of the time devoted to the Twist, were observed outside the main reproductive season. During the main breeding season, visits by females are shorter. In the only two mating visits observed, copulation occurred after a single display sequence, of which the Twist formed a part.

The Twist and the correlative modification of the tail probably evolved together through sexual selection, an evolution that could have been fairly rapid with a socio-reproductive system such as that found in manakins.

Acknowledgments

For the example he has set in thoroughness and attention to detail, we acknowledge our debt to the dean of students of living birds in the Neotropics, Dr. Alexander F. Skutch. We can think of no more appropriate way to express our sentiments than to dedicate to him this article in *The Living Bird* about some lively birds that would warm his heart.

To Captain Jose Obregon we are most grateful not only for friendly hospitality but also for his conservationist attitude toward the natural features of his ranch, Ganaderia Pedernales, where we are conducting the main study of the Wire-tailed Manakin. Our activities spill over into the adjoining Hato El Bufalo, and to its owner, Ivan Faroh, and majordomo, Manuel Peroza, we also express our appreciation.

Stephen Hilty called to our attention a display ground near Ocumare de la Costa and shared with us some observations he had made. Dr. Peter L. Ames and Rosauro Navarro accompanied us in the field on two occasions. Ramon A. Rivero is providing invaluable field assistance in the present phases of our study. Dr. John S. Weske and Charles Janson kindly made available their recordings of the Band-tailed Manakin. To all these friends, our thanks.

Last, but certainly not least, we are indebted to the editor of this journal, Dr. Douglas A. Lancaster, for the patience he has shown during some trying times.

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BEHAVIORAL INTERACTIONS AND NICHE SEPARATION IN BLACK AND TURKEY VULTURES

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In its North American range the Black Vulture *(Coragyps atratus)* is largely sympatric with the Turkey Vulture *(Cathartes aura)*. Furthermore, the foods, roosting places, and nesting places of the two species are similar. I undertook this study to determine the niche relationships between these two species.

Methods

This paper is based chiefly on field observations of activities of free-living populations of Black and Turkey Vultures. Many observations were made from a pick-up truck used for following the birds when hunting food or going to their roosting places. Others were made from concealment in a pick-up camper or an observation blind near feeding places. I spent the daylight hours for six successive days at one feeding site and four days near another feeding site, watching the activities of the vultures. I also spent eight days and nights near two roosting sites watching the vultures coming and going.

Foods and Feeding

Both Black and Turkey Vultures were found feeding largely on visceral and muscle tissues of animals found dead. Turkey Vultures usually fed at small carcasses, while Black Vultures used larger ones. From 5 to 10 May, 1973 I watched a medium-sized steer carcass, at which only Black Vultures came to feed. Thirty-six times, individual Turkey Vultures or small groups flew low over the area without once alighting near the carcass. Furthermore, at six different carcasses of cows being eaten by Black Vultures, I never saw Turkey Vultures approach closely. Even when no Black Vultures were present to interfere with their coming, Turkey Vultures came no closer than 25 meters as they flew low over large carcasses.

Besides having exclusive use of large carcasses, Black Vultures sometimes used large or continuing supplies of small carcasses without Turkey Vultures making any attempt to feed on them. Thus, during the summer of 1975, a flock of about 60 Black Vultures fed daily at a chicken farm where several dead chickens were continually available to the vultures. I saw Turkey Vultures fly low over the area 28 times. They did not land, however, but deferred to Black Vultures in the use of this constant supply of small carcasses.

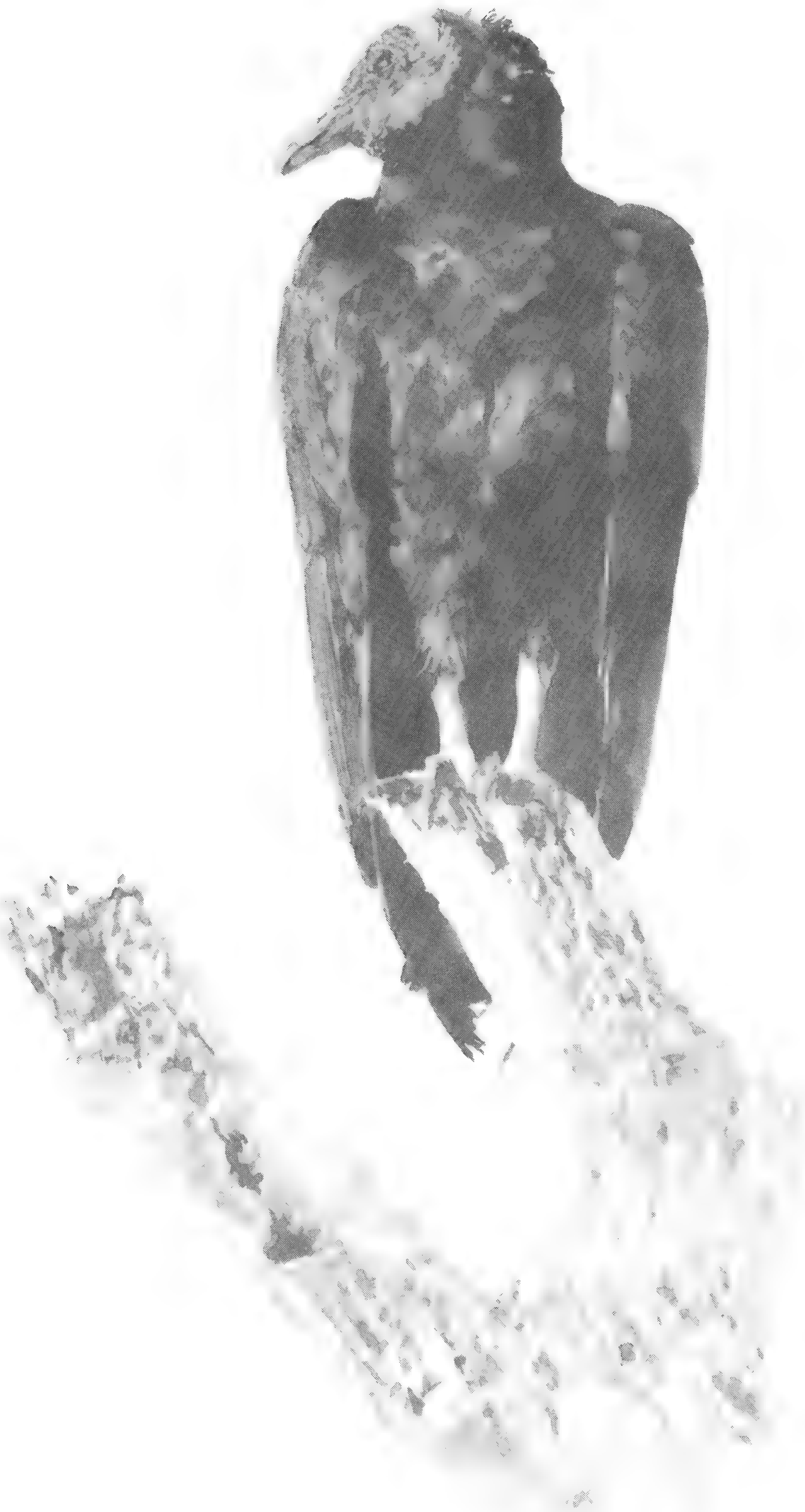
While Turkey Vultures remained away from carcasses at which Black Vultures were feeding, one or several Black Vultures sometimes joined Turkey Vultures in eating carcasses the size of a house cat. The Turkey Vultures usually waited nearby until the Black Vultures finished their eating. Thus, in 48 cases of Turkey Vultures eating at such carcasses, one to three Black Vultures shared in eating at 17 (35.4 percent) of them. Turkey Vultures merely walked away or flew to a nearby post when approached by a Black Vulture at the carcass. Turkey Vultures were never forcibly displaced by Black Vultures. Interference by one or several Black Vultures did not appear to prevent the Turkey Vultures feeding on ample carrion to meet their needs. However, the procurement of food by Turkey Vultures appeared to depend largely on their finding carcasses too small or too scattered to attract more than several Black Vultures. The Turkey Vultures accepted their subordinate status without continued reinforcement, and it can be inferred that the Turkey Vultures' habit of deferring to Black Vultures at large carcasses or continuing supplies of small ones result from habituation to exclusion by Black Vultures.

Black Vultures went to their regular feeding sites soon after daybreak and remained until midmorning, whether or not food was available on a given day. On leaving the regular feeding sites in midmorning, Black Vultures went to other recently used feeding sites or soared high in the sky. The soaring may have enabled the Black Vultures to monitor the food-hunting of the lower flying Turkey Vultures, as scattered Black Vultures were often found during midday eating small carcasses in association with Turkey Vultures. In three cases where I watched, Turkey Vultures came first to such carcasses and Black Vultures followed within 15 minutes. In observations on five species of African vultures, Attwell (1963) noted that some vultures clearly followed others to carrion, with the most common species arriving first.

Although Black and Turkey Vultures were sometimes seen soaring together at the same height, I noted such soaring three times when the birds were near carrion. When carrion was not near, Black Vultures flew much higher than Turkey Vultures. In 48 observations involving soaring vultures of both species away from food sources, at least some of the Black Vultures soared higher than any Turkey Vultures in view.

In their habit of feeding on small scattered carrion, Turkey Vultures seldom returned to the same carcasses for successive meals. In 38 trips over a road running through an area where I often saw both Black and Turkey Vultures soaring and presumably hunting for food, I recorded Turkey Vultures twice as often as Black Vultures. The latter, although present, were gathered at food sources and thus were not soaring.

Also associated with their small-carcass niche, Turkey Vultures hunted food alone or in widely scattered groups of only several birds each. Thus, in sixty-three observations, one Turkey Vulture was seen eighteen times, two were seen twenty-one times, three were seen sixteen times, four were seen eight times, and five were seen two times. On leaving their roosting places in the morning, most Turkey Vultures went individually in various directions. Thus scattered, they spent much time between midmorning and midafternoon flying, with much circling, and mostly within fifty meters of the



Black Vulture, *Coragyps atratus*. Painting by Ted Lewin.

ground, presumably hunting food. Turkey Vultures often did not go directly to carcasses when they found them but continued circling and moving away from the carcass, only to return later.

It seems that Black Vultures are able to discourage, by pressure of their numbers, the use of large carrion by Turkey Vultures. Also, the more robust body structure of Black Vultures may enable them physically to outcompete Turkey Vultures. Black Vultures are slightly heavier than Turkey Vultures; two Turkey Vultures averaged 1,892 grams and seven Black Vultures averaged 2,200 grams.

Black Vultures appeared to monitor the food-hunting activities of Turkey Vultures, and this clue to locating a food source may be the chief basis for association of the two species. This suggests that Turkey Vultures may have some capability for finding food that Black Vultures lack, and it seems probable that this capability may be a keen sense of smell. There has been much discussion and disagreement in the ornithological literature as to the use by vultures of sight and smell in finding food. Much of the disagreement comes from the unjustified assumption that both Black and Turkey Vultures possess the same capabilities. Audubon (1849) made several experiments on food-finding in vultures but failed to indicate whether he worked with Turkey or Black Vultures. Owre (1961) and Stager (1964) have demonstrated that Turkey Vultures use a well-developed sense of smell for finding food; but this has not been demonstrated in Black Vultures (Stager 1964).

My observations support the assumption that Black Vultures lack a keen sense of smell. The regurgitated food I placed beneath a burlap bag beside the active nest of a Black Vulture was left uneaten although similar uncovered food nearby was eaten by a parent bird immediately on arrival at the nesting site. The bird did not even peck at the bag beneath which the regurgitated food was concealed despite the fact that the unconcealed food was quickly eaten. Black Vultures have a strong tendency to eat food regurgitated earlier by another vulture.

Black Vultures possibly may find food by sometimes monitoring the activities of carrion eaters other than Turkey Vultures, particularly dogs. Dogs were present twice at cattle carcasses when Black Vultures first arrived, suggesting that the vultures may have been attracted to the carcasses by the dogs. Also, Black Vultures returned daily to the general area of a site where dogs had dug into the ground and were eating the carcass of a cow buried in a shallow grave, although in 12 hours of watching, I never saw the vultures closely approach the buried carcass. At another time Black Vultures entered a chicken house and upset a garbage can to gain access to chickens being eaten by house cats, possibly having been attracted to the chickens by the house cats. Attwell (1963) also noted that various African vultures find food by monitoring the activities of mammalian predators, and Petrides (1959) reported the arrival of African vultures soon after his killing of specimens of large mammals.

While Turkey Vultures may find food chiefly by using their sense of smell, they also may find food by following other carrion eaters. When I watched a vulture feeding site on 5 September 1975, a Turkey Vulture twice followed two Common Crows *(Corvus brachyrhynchos)* foraging about 35 meters from a chicken I had put out for vultures. The crows moved away when the Turkey Vulture approached them at the first site, only to be followed to a second site. This Turkey Vulture, however, was led to no food by the crows.

Black Vultures sometimes appeared to be attracted to sites with a potential food supply, such as herds of cattle and large chicken farms, even when no dead animals were present. Large numbers of Black Vultures were found gathering at one chicken farm, although the farm operator told me that he knew of no dead chickens available to the vultures. Also, vultures were often seen perched in trees near buildings of what had been a large chicken farm, several years after the chicken-raising business had been discontinued.

Fundamental to the fact that Turkey Vultures surrender food to Black Vultures is the fact that Turkey Vultures are generally more submissive and less aggressive than Black Vultures. The difference in temperament between the two species was apparent even in handling the birds for banding. Turkey Vultures being banded offered little resistance, while Black Vultures were subdued with relatively greater difficulty.

Roosting

I found Turkey Vultures during the spring and summer roosting singly on exposed metal towers supporting an electric power line. Often one or several Black Vultures joined them, whereupon the Turkey Vultures left to seek a less exposed perch in a nearby woods. The Turkey Vultures remained all night on the towers only when not joined by Black Vultures, otherwise moving to avoid roosting in association with the Black Vultures. Both Black and Turkey Vultures were also found roosting communally throughout the year, with congregations often containing members of both species.

Some roosting congregations contained only Black Vultures, particularly those near feeding places used only by Black Vultures. Black Vulture roosting sites were always near active or former food sources. Accordingly, specific sites often were used for roosting only one or several nights. Conversely, where food was continually available, use of the same site was sometimes less temporary.

While the initial selection of sites for roosting seems to be influenced by nearness of food, continued use of a roosting site sometimes results when the birds are protected from disturbance. Vultures continually gather for roosting at the Radford Army Ammunition Plant near Blacksburg, Virginia, where the birds benefit from the limitations on human activity imposed by security regulations. Personnel at the plant stated that the roost had been in continued use over a long, but unknown, period of time.

Associated with the temporary nature of most roosting sites is the smaller size of the roosting congregations, usually fewer than 200 birds. At the Radford Army Ammunition Plant, where the site is in continuous use, the roosting congregation is reported to reach numbers of more than a thousand birds (Prather, *et al.* 1976).

Ward and Zahavi (1973) suggested that communal roosts of mixed species may serve as "information centres," some species following others from their joint roosting places to food sources. In the case of Black and Turkey Vultures, the communal roosts clearly did not serve such a function since the two species often left the roosting sites separately. Without any apparent relationship to their having roosted together, Black Vultures often later found and joined feeding Turkey Vultures. The fact that vultures roosted near feeding sites appeared to result from the fact that the birds fed late in the evening and early in the morning, with the juxtaposition of feeding and roosting sites automatically resulting.

Nesting Places

Black and Turkey Vultures nest in similar situations, both species using hollow logs and trees, caves, old buildings, and dense vegetation on the ground (Brown and Amadon 1968). With both species nesting in such a variety of situations, some of which are abundant in North Carolina, many nesting places are available. With Black Vultures being more aggressive than Turkey Vultures, Black Vultures may exercise first choice in the selection of nesting sites. During the nesting seasons of 1974 and 1975, I examined 18 isolated old buildings and found one of them being used by vultures for nesting, indicating the presence of more than ample potential nesting places to meet the needs of both species.

Summary

Black Vultures in their North American range live in sympatry with Turkey Vultures, and both species use the same types of food, roosting places, and nesting places. Turkey Vultures eat scattered small animal carcasses found largely by their keen sense of smell. Black Vultures eat carcasses which they often find by monitoring the food-hunting activities of other carrion eaters, particularly Turkey Vultures. The more robust and aggressive Black Vultures displace Turkey Vultures from food sources. Turkey Vultures are able to obtain food when living in sympatry with Black Vultures by using scattered small carcasses that do not attract large numbers of Black Vultures. Roosting places were near active or former feeding places, with the nearness of food being the basic factor influencing the selection of roosting places. I found no evidence of a shortage of potential nesting places to meet the needs of both species of vultures.

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SOCIAL BEHAVIOR OF THE AFRICAN COMB DUCK

W. ROY SIEGFRIED

The displays and social systems of most perching ducks (Tribe Cairinini) are known only in broadest outline. The tropical species particularly have been neglected, and as yet have been studied very little in the wild. For the Comb Duck, *Sarkidiornis melanotos*, we have to rely on the fragmentary accounts of Heinroth (1911) and Johnsgard (1961, 1965) who studied captive birds. According to Johnsgard (1961), *Sarkidiornis* (with *Plectropterus* and *Cairina)* characterizes a "generalized" and "primitive" anatinine condition having the following behavioral features: simple displays with the same postures used for aggression and for courtship; copulation achieved by raping of females by the largest and strongest males; and, pair bonds that are practically absent.

This paper describes the displays and associated breeding behavior of the African Comb Duck (Figure 1, Plate 1) in the wild, and shows that the species departs considerably from Johnsgard's characterization. Discussion focuses on preliminary identification of some of the ecological factors which probably have acted in shaping the species' social system and displays. The social system apparently is exceedingly complex, and its complete elucidation offers an exciting challenge to students of eco-ethology.

Methods

I observed and filmed wild Comb Ducks during their breeding and nonbreeding seasons at various localities in Botswana, Rhodesia, southern Angola, and South Africa during the last 20 years. In addition, I have studied the behavior of captive Comb Ducks in waterfowl collections. My observations were confined to birds belonging to the nominate form of *Sarkidiornis*.

In the wild, I was able to identify individual males by differences in the size and shape of the bill protuberance. Differences in facial and flank markings allowed identification of individual females. It must be stressed that none of these birds were marked artificially.

I have followed Moynihan's (1955) definition and convention in identifying and describing a "display": a behavior pattern which is ritualized. Names of some displays are taken from Johnsgard (1965) and McKinney (1965), but other new names are added.

Male Displays

Wing-flap

Wing-flap is one of the most frequent and clearly ritualized movements associated with hostile behavior of both unmated and mated males during the breeding season. A male tends to Wing-flap in immediate response to the proximity of males, and also females, when they approach within about 100 meters of him. A male is unlikely to flap when the subject of his attention is farther away than 250 meters. Wing-flap is usually performed by birds standing on the ground or on boughs of trees, and less frequently while swimming. I have not detected any vocalizations associated with Wing-flap.

The Wing-flap takes the form of a short series of evenly spaced, slow, stiffly executed wing flaps from a stationary posture with the body and head held erect. The number of wing flaps in a series varies, but has not been observed to exceed six ($\bar{x} = 3.4$, 1–6, $n = 48$, male interactions only). In the final flap of a series, although performed most vigorously and resulting in a clapping noise, the wings do not touch each other on the forward stroke. The display is seldom repeated more than once in succession. The male almost always performs the display with his body and head oriented laterally to the male or female for which the display is intended.

A male is likely to respond not only to conspecifics, but also to members of certain other species. I have seen flying Spurwing Geese *(Plectropterus gambensis)*, Blacksmith Plovers *(Hoplopterus armatus)*, and Crowned Cranes *(Balearica regulorum)* elicit Wing-flap. Conceivably, the boldly patterned, black-and-white undersurface of the overflying birds is a strong releaser prompting Wing-flapping.

While the signal function of Wing-flap is clearly associated with long-range threatening behavior by rival males, the significance of the action is not clear in males responding to females. It is possible that the action might function to attract females. However, I have no evidence for this. In all cases ($n = 12$) of males responding to females, the females were flying; and there were fewer flaps per display ($\bar{x} = 2.3$, 1–3) compared to the number in interactions between males. I never saw perched females eliciting the Wing-flap display. Thus Wing-flapping to overflying females may be a case of mistaken sexual identity.

Johnsgard (1965) describes courtship behavior as beginning with "the male deliberately Wing-flapping two or three times in a very conspicuous manner" before going on to perform other displays to the female. In all cases in which I recorded males performing Wing-flapping while associating closely with females, it was a response to and aimed at intruders, usually rival males or overflying females. Following a Wing-flap and successful repulsion of a rival, the male usually gave a Breast-preen display directed at the female if she was next to him. I have not observed Wing-flapping as a part of the precopulatory sequences, and doubt whether Wing-flap constitutes a part of the male's repertoire of courtship displays.

Head-high

This display, also performed by males in aggressive circumstances, is one in which the male maintains an erect posture with head held high and beak pointing slightly upward. The wings are held slightly raised, displaying a conspicuous metallic sheen. The performer's body, neck, and head are oriented laterally to the antagonist beside him.

Head-high is employed by males displaying aggressively and may be seen while the male stands, walks, or swims. This display functions to threaten a rival. A male performing a Head-high advances by stepping or swimming sideways toward his antagonist. The strutting bird steps on the tips of its "toes," utters a hissing sound, and occasionally shakes its tail. This display usually suffices to cause a subordinate male to adopt a submissive attitude and/or to flee. Failure to respond in this manner leads to a Supplant-bow display by the advancing bird.

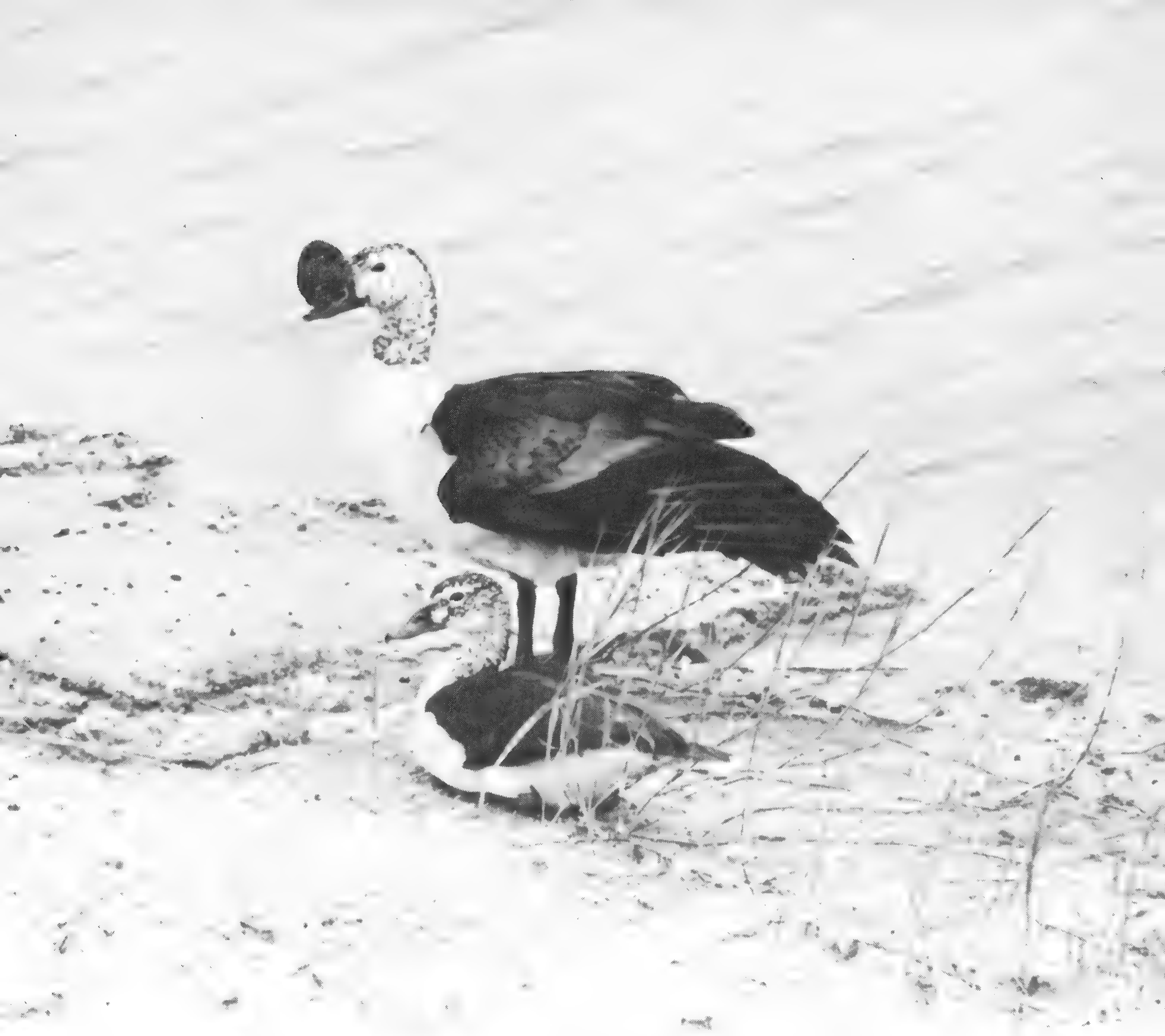

Figure 1. Comb Duck, *Sarkidiornis melanotos.* Found in Africa, South America, and southern Asia, the Comb Duck manifests a marked sexual dimorphism in which the much larger male possesses a large black knob on the bill. The head, neck, and underparts are white. The head and neck are spotted with black. The back, wings, and tail are black and are glossed with green and purple.

A high intensity version of Head-high occurs in flight. A pursuing male flies with his neck, head, and bill held obliquely upward; the subordinate male flies with neck, head, and bill pointing downward. Pursuing males utter a weak, wheezy whistling noise while in a flight.

Supplant-bow

Starting in the Head-high posture, the male performs an exaggerated, stiffly executed, slow bow, moving the head and neck forward and then down under the breast. The wings are held slightly spread and are dragged slightly away from the body; the crest and the scapulars are raised; the tail is fanned. Normally the head is held momentarily under the breast and then raised rapidly while the bird shakes its wings before returning to Head-high.

The display is usually performed by males standing on the ground or on boughs of trees, and less frequently while swimming. If performed while swimming, the bowing movement can end with the bird's head being submerged in the water. On land the bird often reverses direction between bows. On occasion I have heard males utter a soft, wheezing sound while bowing.

Males Supplant-bow in an aggressive context. The functional significance of the display is clearly associated with the act of displacing a rival. A male performing the Supplant-bow usually advances, by stepping sideways, toward his rival. The displaying male's body, neck, and head are oriented laterally to the recipient of the display, which is invariably positioned next to the signalling bird. More than one bowing movement may be required to supplant a rival. Normally, however, a single bow suffices to cause a subordinate to adopt a submissive attitude and/or to flee. Less subordinate or equally ranking rivals may respond by performing one or two Supplant-bows before fleeing or, in rare instances, by remaining in place to engage in combat.

Wing-shake

Ritualized Wing-shaking occurs during hostile encounters and is closely associated with Supplant-bow. A male Wing-shakes to threaten another male in close proximity. The display is given while a male is standing sideways to his rival. The wings are shaken well away from the sides of the body.

Body-shake

What appears to be ritualized Body-shaking occurs in pair-bonding situations and is linked closely with Breast-preen. The male orients his body laterally to the female, performs a body-shaking movement, preceded by a Tail-wag, and immediately bends forward to nibble his breast feathers. However, the shake can also occur independently of Breast-preen. In such cases, ritualized Body-shaking appears incomplete in that it does not end with rotation of the head. Instead, the head is jerked upward.

Breast-preen

In this display the male performs a stiffly executed, slow movement, bending the neck and lowering the head to briefly nibble the feathers in the lower breast. The wings are held slightly spread and away from the body. Immediately after the preening movement, the male raises his neck and head, keeping the beak pointing downwards and close to his body. The display is usually preceded by a ritualized shake; the male's body is deliberately oriented laterally to the female. Because of this display, the breast can be quite bare of feathers in the nibbled area. The display is normally not repeated more than once in succession.

Breast-preen is the most frequent and clearly ritualized action associated with courtship and pair-bonding behavior. Males give the display on land, boughs of trees, and less often in water, and only in the close proximity of a female. A swimming male performing the display submerges his head in the water. I have not detected any vocalizations associated with Breast-preen.

Head-down-end-up

In this display, the male draws in his head and holds his bill, pointing downwards, against his breast; the wings, slightly spread, are raised posteriorly. The male holds the posture stiffly for several seconds while aligning his body laterally to a female; his bill can be turned slightly off-center, pointing away from the female. The male may be swimming or standing in shallow water or on dry ground. I have not heard any vocalizations accompanying the posture.

The male performs this precopulatory display before the female adopts the prone position. The same, or a very similar, posture also forms the male's main post-copulatory display.

Drinking and Turning-back-of-head

I have noted exaggerated and what may be ritualized drinking movements on a few occasions. In all cases the movements were performed by males approaching females. I have seen drinking only once in a precopulatory situation. This contrasts with Johnsgard's (1965) contention that when approaching and courting a female, "males often perform a single Drinking movement followed by a turning of the bill slightly away from the female." Johnsgard equates this turning away of the bill with a rudimentary Turning-back-of-head. I am still uncertain as to the precise form of this display in *Sarkidiornis*, but apparently an "incipient" form of the behavior does occur.

Preen-behind-wing

McKinney (1965) and Johnsgard (1965) report Preen-behind-wing in the South American Comb Duck, *S. m. carunculatus*. According to Johnsgard, the display is used in courtship, usually following a Breast-preen, the male "bringing his bill down and Preening-the-breast-feathers ... and finally turning his head to place the bill behind the wing closest to the female and performing a single, slow Preening-behind-the-wing movement."

I have not seen anything in the African Comb Duck to indicate that Preen-behind-wing is involved in sequences of courtship behavior involving Breast-preen. Preening-behind-wing movements do, however, occasionally follow Breast-preen, but they appear to comprise unritualized, normal comfort behavior. I have noted only two instances in which a Preen-behind-wing perhaps constituted ritualized behavior. In both cases the bird preened behind the wing nearest to the other bird, who was a threatening male. The preening movements occurred in a hostile situation, and were given by subordinate males apparently in response to aggressively dominant males. Thus, the possibility that the action may constitute part of the male's ritualized submissive or appeasement behavior should not be discounted.

Agonistic Behavior

Submissive Posture

Subordinate males usually respond to a dominant bird's threat displays by adopting a submissive posture. Typically, the subordinate presents a sleeked plumage, and crouches (when on land or in a tree) with tail down, head and neck drawn in, and bill pointed downward and slightly away from the aggressor. The posture is normally performed in response to a dominant male's Head-high and Supplant-bow displays.

Threat

Apart from Inciting, females threaten males and members of their own sex by adopting an erect posture with bill up, wings slightly raised, and nape feathers erect. A harsh *guk-guk* call may be given. A female with a brood threatens intruders in this way; so does a paired female when confronting strange, single females that may be attempting to lead away the mated male. Bill-gaping occurs in overt threatening behavior.

On three occasions I saw females threaten other females and, in the process, perform movements identical or similar to the Supplant-bow of males. These interactions involved females busy inspecting and selecting nest-cavities. Females also have been observed fighting each other. They adopt postures similar to those of males and strike each other with their wings.

Hostile Encounters

A breeding male with one or more females is intolerant of the presence of other males. The male's repertoire of hostile displays includes Wing-flap, Head-high, Shaking, Supplant-bow, and fighting. These behaviors are given in the following typical situations. The breeding male, either alone or in the company of his female(s), first responds by Wing-flapping to an intruder (usually flying) when the rival is still some distance — about 150 meters—away. Closer approach by the intruder usually elicits pursuit. The intruder normally does not respond immediately by fleeing, but awaits the close approach of the aggressor. The aggressor adopts the Head-high posture in approaching his rival. If the intruder does not respond by fleeing, the aggressor performs additional threatening actions involving Shaking and Supplant-bow, in that order. This sequence culminates in fighting when the intruder stands his ground and matches the aggressor's Head-high, Shaking, and Supplant-bow displays. However, in most hostile encounters the intruder responds to Head-high by first adopting, and apparently retaining for as long as possible, a submissive or appeasement posture before terminating the interaction by fleeing. Reluctance by the intruder to flee more than about 100 meters from the scene of the encounter leads to renewed pursuit and threatening actions by the aggressor. Repeated sequences of this sort are common. Normally the breeding male returns to his female(s) and performs a Breast-preen display immediately after termination of a hostile encounter.

Fighting

Fights develop rarely and apparently only between males that are more or less evenly matched and are competing for females. Fights may last up to a minute or longer (maximum duration observed = 65 seconds) and may involve vigorous bodily contact. Most fights occur on land (13 times); some take place on water (3 times); only once did I see males fighting in a tree. All fights on land begin with the rivals holding their heads below their breasts in the Supplant-bow posture while circling each other with a slow stiff-legged, sideways gait for about five seconds. In high-intensity encounters, the rivals utter a sound similar to the creaking of an unoiled wagon wheel. These temporary stalemates are broken when one male suddenly lifts its head and attacks from a Head-high posture. The males face each other and, with bills pointing slightly upward, rear up and strike with their wings. They thrust and bump against each other with their breasts. The combatants do not use their bills to grip or peck each other. The contest ends with the victor causing his rival to lose balance and topple over or to retreat. The victor pecks at the vanquished bird as he escapes. The result of a fight is decisive and apparently final, for the loser remains subordinate to the victor in future agonistic encounters.

Female Displays

According to Johnsgard (1965), "The female of this species is a remarkably quiet bird, uttering at most a very weak quack when disturbed or frightened." In my experience, female African Comb Ducks can be very vocal at times, particularly during the early part of the breeding cycle when they are seeking mates and breeding sites. I have recorded distinctive sets of vocalizations identifiable by their characteristic quality and by the contexts in which they occur.

Inciting

The female has a true Inciting display. Quick chin-lifting movements are performed by the female who calls with a soft clucking *guk-guk*; the open bill points toward the non-desired male.

Coquette-call

The female repeatedly utters a soft, melodious *caroo-oo* (similar to the "purring" call of the female domestic Muscovy) while bending her head and neck forward and down, along the side of her breast. The display is similar to the Coquette-call found in *Aix* (see Heinroth 1911).

Going-away-call

The form of this call and the context in which it is uttered vary, as in many Anatinae. The note most often heard is a loud, frog-like *hu-ark* given repeatedly by females on the wing while prospecting for nest-sites. The call is also given at times in the typical "going-away" situation involving a mated female flying away from her male. I observed single (unmated) females walk or fly to mated or unmated males and then deliberately turn and fly off in front of the male, apparently attempting to elicit a following response. On numerous occasions I noted single females calling *hu-ark* repeatedly while flying toward feeding groups of mated males and females. The females, apparently soliciting, first circled low over the groups and landed close to the males, which they then apparently attempted to stimulate into chasing after them. In cases in which males do not respond by following, females may repeatedly renew their solicitations with short circular flights away from, and back to, the male. In some cases in which males followed females, the female repeatedly uttered the *hu-ark* call once both birds were airborne. In these flights, and in others, the female's white rump shows conspicuously and this could have signal function in leading the male. The male has a duller, grayish rump.

Other Vocalizations

A soft, whining call is uttered repeatedly by females while feeding in the company of their mates, especially when the birds are in dense emergent vegetation. A louder, sharp, single squealing call apparently functions as an alarm or warning signal.

Repulsion

The female Comb Duck's posture in this display conforms to that given typically by the Mallard, *Anas platyrhynchos*, and other Anatinae. I have not observed "repulsion flights" at distances close enough to be able to identify the female's vocalizations.

Breast-preen

Females very occasionally perform breast-preening movements, linked with Shaking, apparently in immediate response to Breast-preen by their mates. I am uncertain as to whether these breast-preening movements constitute ritualized behavior in females.

Copulation

Normal copulation between a mated male and female involves actions no more awkward or forceful than are found in most Anatidae. The male adopts the Head-down-end-up display in his approach to the female. If receptive, she responds by assuming the prone position, with neck and head stretched on the water, soliciting copulation. Apart from this, I have not observed Head-pumping or any other precopulatory behavior on the part of both birds. Nor have I observed the male pecking at the dorsal surface of the female prior to mounting. The male mounts from the side, gripping the female's nape. Treading normally lasts only a few seconds. The male dismounts forward over the side of the female and swims or walks, somewhat rapidly, more than a meter away. During his brief swim or walk, the male lifts his tail and holds a general posture that is the same as, or similar to, Head-down-end-up. I have not detected any vocalizations during post-copulatory behavior. Nor, in ten copulations, did I see the male bathe after a post-copulatory swim. In one case the male wing-flapped. After the male has dismounted, the female immediately performs vigorous wing-flapping movements and then either bathes or continues feeding together with her mate. All ten copulations occurred with birds standing in shallow water (3–10 cm deep) or swimming in deeper water.

Social System and Associated Breeding Behavior

In southern Africa, the Comb Duck breeds from December to March, during and following the period of summer rainfall. Although relatively few banded birds have been recovered, regular seasonal movements over long distances clearly take place (unpublished records filed at the South African National Unit for Bird Banding Administration, University of Cape Town). With the onset of the rains, the winter (dry-season) flocks break up and the birds disperse to breeding areas. Marshes and temporary pans in woodland and woodland-fringed lagoons of inundated floodplains offer suitable and apparently preferred breeding habitat (Figure 2). An important feature of the Comb Duck's breeding grounds, at least in southern Africa, is the variable nature of the intraseasonal rainfall. This influences the rate at which flooded pans dry out, contributing a degree of unreliability in the breeding habitat because future rainfall during the season is unpredictable.

Nest-site Selection

Comb Ducks nest in cavities in trees, and the same cavity may be used in successive years (McLachlan and Liversidge, 1970). In Africa, the fringes of woodland bordering on pans and lagoons are heavily used by elephants, and tend to support numerous dead and hollow trees (Anderson and Walker

1974). The trees are damaged initially by elephants, and subsequently by wood-boring insects. Thus, potential nest cavities tend to occur relatively close to water, and the dead trees serve, additionally, as perches for the breeding birds (Figure 3).

Prospecting for, and inspection of, a nest cavity is the activity of the female, which flies from one likely looking tree to another. Every tree is inspected thoroughly, the female clambering along branches and peering into all crevices. I recorded individual females spending up to 20 minutes carefully peering into individual holes. This behavior should be viewed in relation to the risk a female runs in descending into a dark cavity that may hold a snake or other potential danger.

Females search for cavities at all hours of the day, but concentrate on this activity for about three hours in the early morning on consecutive days. I have no information on the amount of time that an individual female invests in searching for a cavity in any one particular area. The inability of a female to obtain a nest site in a given area is determined by the absence of suitable cavities in that area or by the existing cavities being pre-empted by other females. Competition between females for cavities apparently occurs; and I have observed hostile encounters between prospecting females. Initially unsuccessful birds moved up to five kilometers away and began searching anew.

Although nests are situated sometimes as much as one km from water (McLachlan and Liversidge 1970), they generally are closer (pers. observ.). Conceivably, it is advantageous for a female to nest close to a body of water suitable as a feeding and brood-rearing area. Thus, an association of three components—nest cavity and feeding and brood-rearing areas—determines the quality of the breeding habitat.

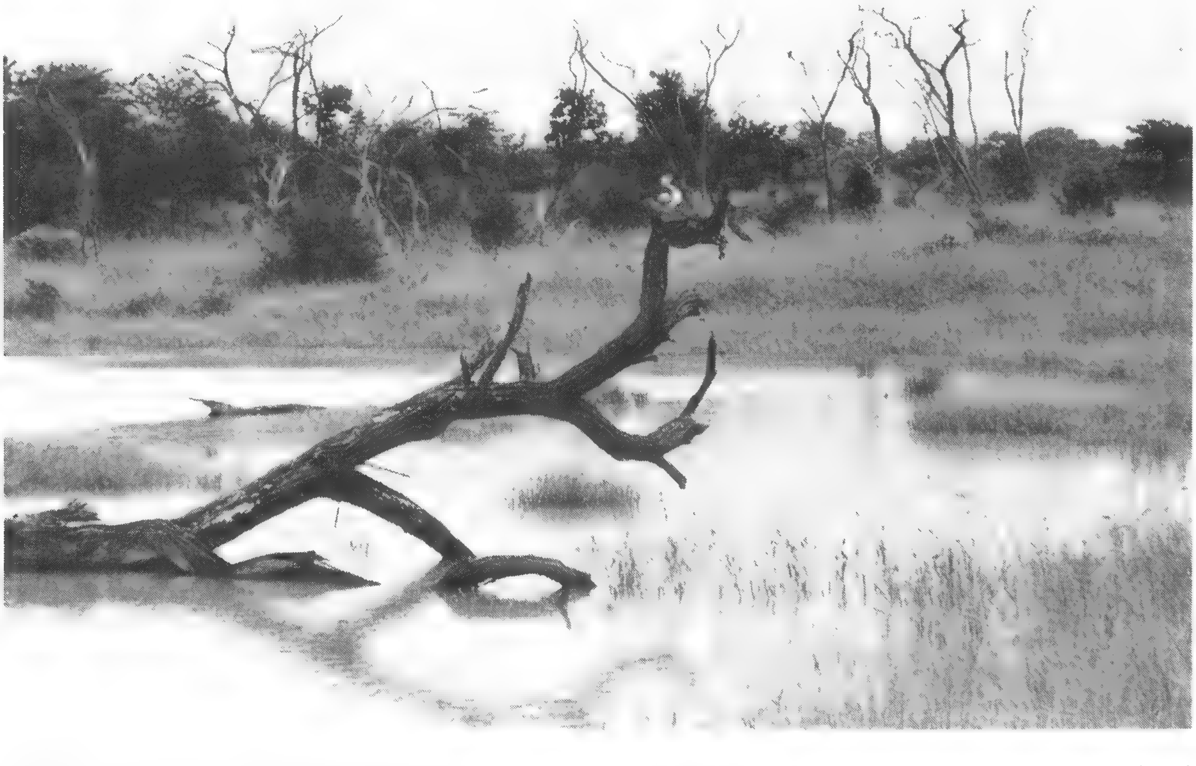

Figure 2. Favored breeding habitat for the Comb Duck includes marshes and woodland-fringed lagoons.

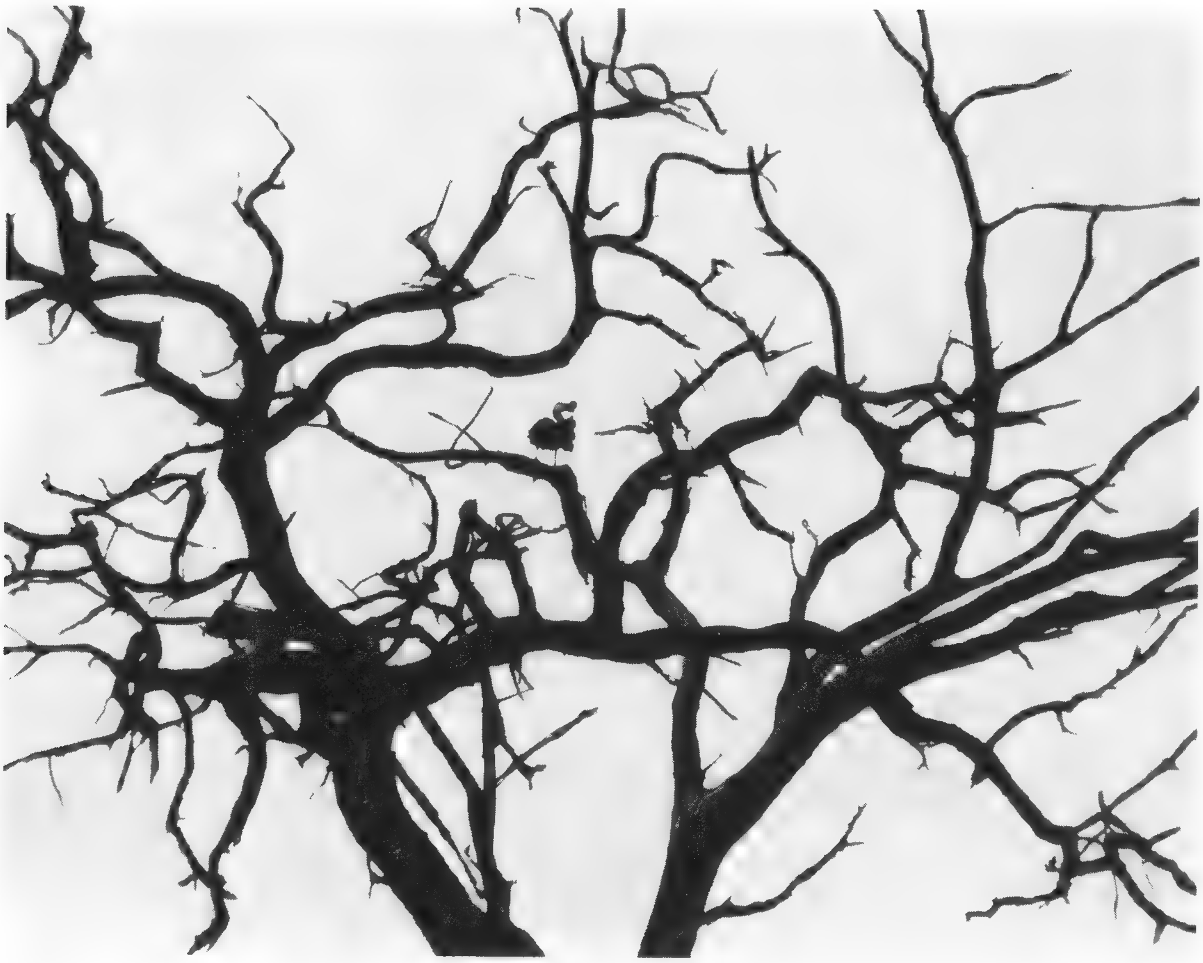

Figure 3. Dead trees with cavities offer nesting sites for the Comb Duck and serve as perches.

Territoriality

The breeding female and her mate tend to restrict their feeding and loafing to one particular area. The male remains strongly attached to this site, seldom leaving it as long as his mate(s) uses it and continues to associate with him. He defends his mate(s), and consequently the area she is in, against all intruding males. He also acts aggressively by threatening and chasing males out of his "territory" when his female(s) is not with him. The area from which intruding males are excluded normally extends over a radius of about 150 meters, with the "owner" and/or his mate(s) at the center. The defended area lacks a fixed boundary and may be a moving one along a line of 800 meters or more of wetland, depending on local topography.

Mating System

Within the limits of the Republic of South Africa there are no major tropical flood-plain systems, and areas of seasonally flooded, savanna woodland are restricted. In the main, the region offers only marginal habitat for breeding Comb Ducks, which are distributed sparsely and generally occur in pairs. Probably this underlies the statement by McLachlan and Liversidge (1970) that for the Comb Duck there is "... no evidence regarding polygamy in southern Africa." However, polygyny is normal in Rhodesia and other territories to the north of South Africa (pers. observ.).

The Comb Duck's mating system embraces monogamy, harem polygyny, and successive polygyny. In harem polygyny, one male has a pair bond with two or more females at the same time. In successive polygyny, one male has bonds with two or more females in succession. Individual males can be involved in both harem and successive polygyny during the course of a breeding season.

Pair bonds are formed in the breeding areas. However, it is not known whether this is universal, and it might be that some individuals form bonds elsewhere early in the season. The sexes are segregated to a large extent during the non-breeding season (Clancey 1967; pers. observ.). Unmated females have been observed to approach and stimulate males into following them in flight. Mated and unmated males occasionally respond by following such females. Conceivably, these are females who, having located suitable breeding habitat, are bent on leading males to these areas and obtaining their services as mates. A dominant mate is important to the breeding female, since it is his influence that permits her to feed and loaf in relative security in the area chosen for these activities. It is not known how long individual pair bonds persist, but certainly the bond endures throughout the laying period of a female's cycle, and incubating females continue to associate with their mates as long as they remain "on territory."

If there are sufficient resources locally to induce females in varying stages of the breeding cycle to settle temporarily, and if it is subsequently advantageous for these females to form bonds with a male in his territory, then that male can remain attached to one particular site for many weeks, which may span the entire breeding season. Such males are harem-masters. In addition to other aspects attending his relative superiority as a breeding partner, a harem-master's prolonged attachment to a particular site could benefit brood survival; broods raised by females in an area under continued vigilance of the master should be relatively more efficient at feeding and other activities because of the absence of marauding males and predators. Both partners stand to profit through such an arrangement, which need not necessarily involve the male in an extension of the pair bond *per se* or in participating directly in raising the young. I have not observed males caring for ducklings or assisting the female in doing so.

Within the harem, one particular female has "queen" status, with the bond between her and the male being relatively strongest. The association between the queen and her mate is a close one. The two birds tend to follow each other and to feed and loaf more closely together than either does with any other member of the harem. In harems, it appears that matching of activities and proximity of associations between male and female operate according to an exponentially expanding order, with the queen at the head of the females and each supplementary female occupying a distinct place in the order.

The biggest harem I recorded consisted of four females. I have seen individual harem-masters accompanied by as many as ten females, but there was no way of knowing whether all the females were mated to the one male. Single, presumably unmated, females temporarily join harems, associating loosely with their members while feeding and loafing. These females presumably profit by these temporary associations through increased predator awareness and detection, and escape from the attentions of unmated males. The result would be enhanced feeding and loafing efficiencies. The mated females usually tolerate the presence of such strangers, which are, however, relegated to relatively low stations in the females' dominance order. The harem-master's reaction varies: outright acceptance and tolerance, courtship, and overt aggression with or without intention to rape have been observed. The harem-master's reactions may be influenced by the size of his harem, the reproductive state of his females, and their reaction to the newcomer. There presumably are occasions when he has to make a "difficult decision" on whether to accept a new recruit or to reject her, since the larger the harem the more unwieldy it becomes. It creates enhanced opportunities for rival males to gain access to the females, and could result in the master losing his entire harem. Similarly, the mate-seeking female must "gamble" on the male of her choice. A master with a large harem offers immediate superior fitness, and with it a high-quality breeding habitat, but in some cases the female may do better to bet on joining a male with a smaller harem.

Competition for the Harem

A harem-master has to contend with severe competition from unmated males. These rivals continuously "test" the master in attempts to either rape his females and/or to dispossess him of his favored position. A defeated master loses his territory and his females to the victorious male. A master who even slightly neglects the protection of his mates impairs his investment, presumably in so far as his genetic contribution is "diluted" by rapists whose harrassment of females could lead to their deserting the area. The harem-master spends most of his time on three activities: feeding, loafing, and watching for, and interacting with, rivals. Of crucial importance to a master's success is his ability to synchronize his feeding and loafing spells with those of his females. A harem which ceases to maintain its close integrity is immediately beset by rapists. Consequently, the harem fragments and the harem-master's attentions are drawn from one female or rapist to another, which has the effect of enhancing the rapists' opportunities. Apparently, the ideal situation for every member of the harem is to remain close together and to feed and loaf as a group. Even for copulation, the group does not normally divide, the two partners copulating within the group.

Tables 1 and 2 present data on the activities of two harem-masters. Feeding was clearly the major activity, which tended to slacken in the middle of the day. These schedules do not include time spent on interacting with rival males, but do show (Table 2) that feeding and loafing spells were interrupted frequently by the actions of rivals. The majority of these interactions involved supplanting behavior and associated aerial pursuit by the harem-master (Table 3). I estimated that Male A covered about eight km per day and Male B eleven km per day in pursuit flights during the course of a normal day. In terms of time, each harem-master spent an average of about one hour per day interacting with rivals. Individual pursuits covered relatively short distances, tending to involve "round" flights of about 300 meters (from female to rival and back to female). Longer flights were unusual and presumably are maladaptive, in that the harem-master cannot afford to risk leaving his females and exposing them to additional would-be rapists. The harem-master's tactic must be one of immediate reaction, short and vigorous pursuit, and rapid return to females. This behavior must be taxing energetically for such a relatively large and heavy bird as a male Comb Duck. This might be an important factor favoring the selection of Wing-flap as a long-distance threat display. Also, perhaps, the presumed heavy energy drain attending repeated pursuits can be related to the considerable amount of time spent feeding. A feeding spell of a harem-master averaged 79 minutes (S.D. 38, range 160–24, $n = 13$) and an average loafing bout was 34 minutes

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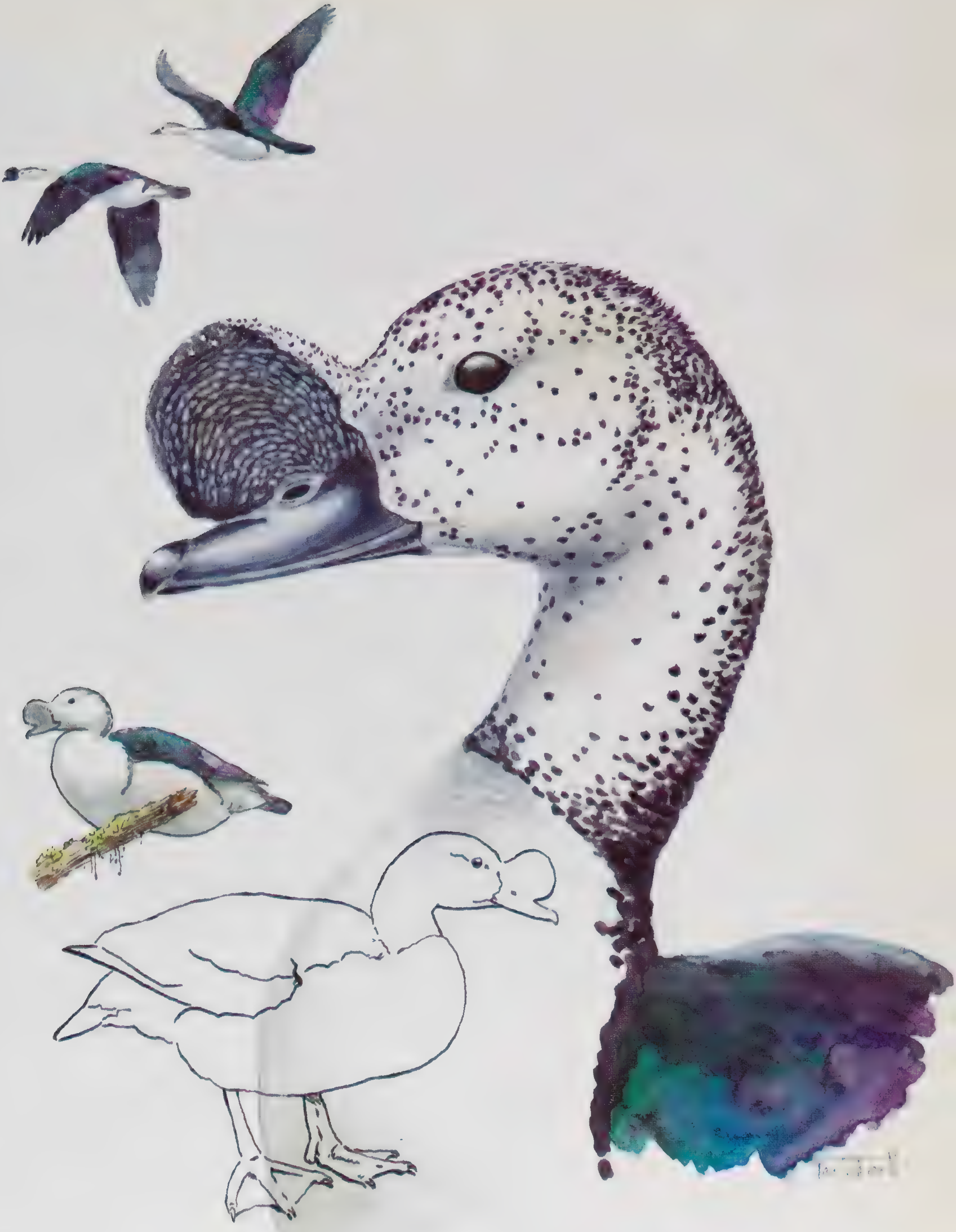
Comb Duck, *Sarkidiornis melanotos*. Painting by Terence M. Shortt.



Knob-billed duck ♂
Sarkidiornis melanotos
Budongo Forest, Uganda.
3200 ft

TABLE 1

Time Spent Feeding and Loafing

Time of day	*Percent of time spent**		*Number of hours of observation*
	Feeding	*Loafing*	
Male A			
0600–0900	87	13	6.3
0900–1200	54	46	6.2
1200–1500	52	48	7.0
1500–1800	87	13	16.5
1800–2000	69	31	5.8
Male B			
0600–0900	85	15	6.7
0900–1200	79	21	6.3
1200–1500	50	50	2.7
1500–1800	71	29	13.7
1800–2000	62	38	2.7

	Mean number of hours per day		*Percentage of loafing time spent in trees*	*Number of hours of observation*
	Feeding	*Loafing*		
Male A	9.8	4.2	70	42
Male B	10.0	4.0	61	32

*Mean time of two harem-masters, each with three females, at Wankie National Park, February 1974.

(S.D. 30, range 120–12, $n = 15$). Loafing bouts of the harem's individual females tended to be longer ($\bar{x} = 48$ min., S.D. 25, range 85–10, $n = 11$). A female's feeding spells averaged 84 minutes (S.D. 30, range 120–35, $n = 13$).

Feeding

Comb Ducks feed mainly by dabbling in mud and by stripping grass seeds while wading in shallow water. There is a hint that mated females devote more time to dabbling than their harem-masters who appeared to concentrate on seeds. In two separate harems in which I observed the members feeding together, the males tended to strip seeds while the females (three in each harem) concentrated on dabbling. The difference in feeding behavior may reflect nothing more than the male's greater size, permitting him to reach seed-heads somewhat more easily. On the other hand, it seems likely that the segregation is related to a difference in the physiological requirements of breeding males and females. The females, especially those in the process of forming eggs, require a relatively higher protein intake, presumably obtained more efficiently by consuming protein-rich invertebrates. The harem-master's relatively high energy demands brought on by repeated interactions with rivals could be met most efficiently through feeding on carbohydrate-rich grass seeds. Furthermore, the sexual segregation, with respect to feeding, might allow the area occupied by the harem to support more females or make available to the harem females a greater quantity of food when they need it most.

Protection from Rapists

Comb Ducks usually feed in flooded emergent vegetation a little taller than the birds. In this situation females seem to be especially vulnerable to aerial predators and to rapists, who keep watch from elevated perches in trees surrounding the water, and from which they descend on unsuspecting and unprotected females. A harem-master remains very watchful while feeding with his mates. He frequently adopts an alert posture, peering around to check on the presence and positions of his females and rival males. Females perched in trees suffer less harrassment from would-be rapists than females either feeding or loafing on the ground. The tree aspect also affords a loafing female a better opportunity to detect rapists and to escape from their overt attentions. Table 1 shows that harem-masters spent most of their loafing time in trees, and this is an indirect measure of the tendency of their mates to loaf also while perched in trees. In this context, it may be pertinent to comment on how well the birds' predominantly gray-black plumage pattern blends cryptically with the gray-black wood of dead boughs on which the birds normally sit.

Termination of the Bond

The break in the bond between a vanquished harem-master and his queen was observed, in one instance, to take place gradually. At the time of the break, the queen was in the laying stage of her cycle. She had been raped by the new harem-master on the day previous to the decisive fight between her mate and the rapist. Following her mate's defeat and his immediate and complete loss of territory and all supplementary females (two), the queen spent time alternately with each male. She quite deliberately left the harem and its immediate environs temporarily to seek out her former mate, who followed and accompanied her closely during bouts of feeding and loafing. These observations support the contention that bonds between individual males and females can involve a degree of mutual attraction and faithfulness. After two days of divided association, the queen completely deserted her first mate and became a full member of her new mate's harem. However, she no longer headed the females of the harem. Her former mate tended to remain in the area for another three days, during which he, and other single males, periodically attempted to gain access to the harem. The defeated male adopted subordinate status in all encounters with the new master.

Activities of Unmated Males

The polygynous mating system results in a surplus of unmated males; it is not the result of a surplus of females. In a series of counts of Comb Ducks in Wankie National Park, Rhodesia, during the breeding seasons of 1973 and 1974, totals of 163 females and 172 males were obtained. This sex-ratio does not depart significantly from parity.

Unmated males tend to cluster around the territories used by harems. At any one time, there were usually between one and four such males in the proximity of the two harems which I studied intensively. These rivals typically spent much of every day at one particular harem-master's territory, rather than moving from one territory to another and spending a little time at each one. The birds visiting any one territory apparently recognized each other and tended to adhere to a system of rank.

TABLE 2

Mean Frequency of Agonistic Encounters

Interactions	*Male A*	*Male B*
Mean number of interactions per day*	61	56
Mean rate of interactions during:		
Feeding spells	1/14 min	1/18 min
Loafing spells	1/13 min	1/11 min
Mean number of supplanting flights per day	26	33
Mean rate of supplanting flights	1/32 min	1/25 min

*Sample was taken in February 1974 at Wankie National Park, Rhodesia and included two harem-masters, each with three females, and unmated males.

Subordinate males gave way to dominant individuals in their approaches to females and in competition for favored perching places in trees. It may be advantageous for an unmated male to stay in the vicinity of a harem-master's territory, because this stratagem maximizes his opportunities for courting unmated females and/or raping mated females who are laying eggs or about to lay. Unmated males normally concede almost immediately, and quite peacefully, to the harem-master when aggressively challenged by him. In these agonistic encounters, the subordinate usually does not flee immediately. Instead, his appeasement behavior allows him to remain in the area and relatively close to the harem. Tinbergen (1959) made the point that appeasement signals may be motivated to varying extents by fear and a desire to stay. In many interactions between harem-masters and their rivals, the harem-master employed the Supplant-bow — his most potent display short of actual combat—before the appeasing rival fled (Table 3). Typically, such flights occurred over relatively short distances (50–100 m), causing the harem-master to re-engage in pursuit and subsequent supplanting behavior. Thus, the would-be rapist watches and waits near the harem, and moves in on a female whenever the slightest chance is offered.

TABLE 3

Relative Frequencies of Displays
and Incidence of Agonistic Encounters

Interactions	*Male A*	*Male B*
Number of interactions recorded*	93	57
Number of interactions involving only Wing-flap	34	14
Number of interactions involving supplanting	59	43
Percentage of supplantings		
In air	7	14
In trees	40	45
On land and water	53	41
Involving pursuit flight	70	76
Involving Supplant-bow	67	52
Percentage of Supplant-bows in trees	45	73

*Sample consisted of two harem-masters, each with three females, and unmated males at Wankie National Park, February 1974.

Males with large harems appear to be less successful than males with smaller harems at protecting their females from rapists. Thus, one might expect unmated males to congregate near the larger harems. There are hints that this is in fact the case, but I lack quantitative data. The more rivals a harem-master has to deal with simultaneously, the greater the opportunity for any one of the unmated males to succeed in raping a member of the harem. The would-be rapists' "tactics" in gaining access to females vary and involve such contrasting behavior as long, patient, crouching sneaks through cover to direct dives from the air. It appears that the more blatant, bold, and direct approach is favored most often by males who have relatively high-ranking social status. My observations suggest that these males attempt to rape only mated females, which they distinguish from the unmated females to whom they normally display courtship behavior. This presumed ability of males to perceive the difference in mated status of various females might be related to the fact that unmated males concentrate their activities in one area.

Discussion

The Comb Duck has a repertoire of distinct displays, with clearly different signal postures used for aggression and courtship. The species' social organization is complex, with several variations attending competing interests of individual birds and conflicting selection pressures. A comprehensive review integrating the communication methods into the social organization would be premature since I lack firm evidence for demonstrating how the system works. There are, however, several indications that the Comb Duck's close association with trees is fundamental to the ecology-behavior evolutionary relationship.

Relationship Between Arboreal Habit and Behavior

Comb Ducks spend much time in trees. It seems likely that the emphasis on sideways posturing by displaying birds evolved in response to the species' arboreal habits. The male's signal postures, without exception, are performed while the sender orients his body laterally to the recipient of the signal. Changes in body posture during displays involve mainly slow, deliberate bowing and sideways-stepping movements. All movements are somewhat stiffly executed, apparently so as not to impair the sometimes precarious balance of the perched bird. Sideways stepping is an ideal form of locomotion for moving along a branch of a tree. The absence of the use of the bill to hold onto a rival appears to be an adaptation for fighting while perched in a tree. Since the outcome of a fight depends on one of the contestants being forced into losing his balance and toppling over, it seems important to avoid any form of locking contact, as could occur if the rivals used their bills to grip each other. This might result in both contestants falling from a branch.

Polygyny and Habitat

Orians (1969) advanced a theory to explain both the scarcity of polygyny among birds and the conditions under which it should be expected to evolve. The theory places emphasis on the leading role of the female in choosing a mate from available males. The consequences of polygyny include increased selection for sexual dimorphism, usually manifested by larger males with

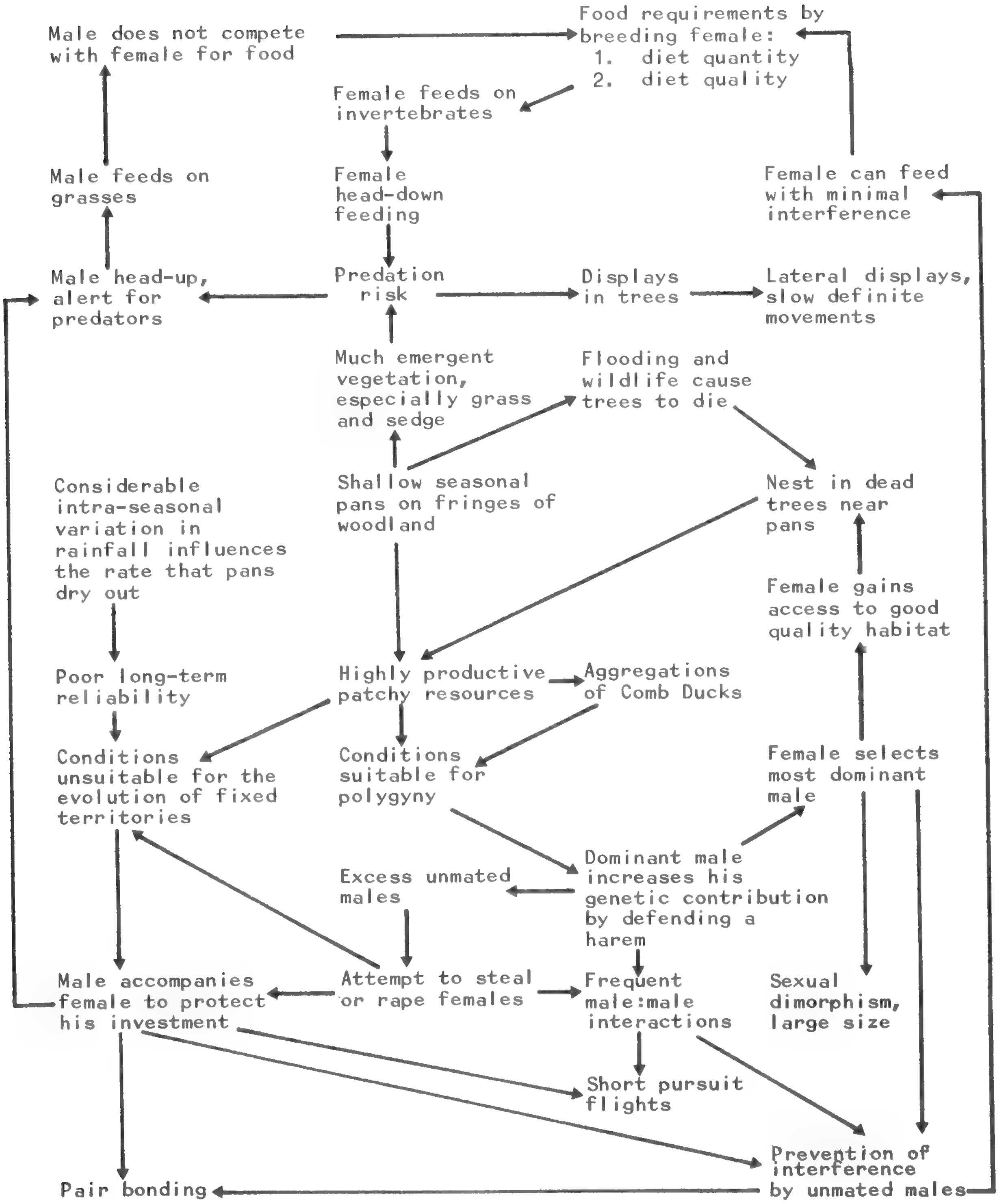

Male does not compete with female for food
Food requirements by breeding female:
1. diet quantity
2. diet quality
Female feeds on invertebrates
Male feeds on grasses
Female head-down feeding
Female can feed with minimal interference
Male head-up, alert for predators
Predation risk
Displays in trees
Lateral displays, slow definite movements
Much emergent vegetation, especially grass and sedge
Flooding and wildlife cause trees to die
Considerable intra-seasonal variation in rainfall influences the rate that pans dry out
Shallow seasonal pans on fringes of woodland
Nest in dead trees near pans
Female gains access to good quality habitat
Poor long-term reliability
Highly productive patchy resources
Aggregations of Comb Ducks
Conditions unsuitable for the evolution of fixed territories
Conditions suitable for polygyny
Female selects most dominant male
Excess unmated males
Dominant male increases his genetic contribution by defending a harem
Male accompanies female to protect his investment
Attempt to steal or rape females
Frequent male:male interactions
Sexual dimorphism, large size
Short pursuit flights
Prevention of interference by unmated males
Pair bonding

Figure 4. Suggested relationships of the various behavioral and ecological factors involved in the Comb Duck's social system.

enhanced secondary sexual characteristics, such as the bill protuberance of the male Comb Duck.

Orians' model predicts that a female will favor an already mated male as a mate if that male occupies a territory containing resources superior to those offered by other males. This is, in fact, the case in a number of polygynous species (Orians 1969), in which unmated males directly compete for discrete territories embracing restricted and/or varying resources such as feeding and/or nesting sites to which females are attracted. This implies that both sexes must be able to perceive, and to discriminate between, variation in the quality of the breeding environment.

The Comb Duck breeds when the climate is hot and wet; and spatial and temporal variations in breeding habitat may be great. Rainfall is relatively high, but precipitation is unevenly distributed annually, seasonally, and locally. Many Comb Ducks do not breed in years of poor rainfall (pers. observ.). These ecological conditions should favor the evolution of polygyny, since differences in the quality of the breeding habitat presumably are great enough to make it advantageous for females to mate with males in optimum habitat, rather than with unmated males in poor habitat. If the species is long-lived, which may be the case, then there should be selective pressure for nest-site fidelity by females. The female's choice of a mate should be based on his genetic quality and that of his territory. I suspect that a queen, or primary, female first selects her mate largely on the basis of his "dominance" and independently of quality of breeding habitat. The members of the pair then use physiognomic cues in assessing and selecting the breeding habitat in which they settle. Secondary females should use mainly physiognomic cues in assessing the quality of the breeding areas controlled by mated males.

While much remains to be learned about the Comb Duck's strategy for optimum reproduction, and its relationship to Orians' (1969) theory, it appears that unmated males do not establish territories containing nest sites or feeding areas. Presumably, the distribution of nest cavities is such, especially in respect to variation in distance separating cavities and feeding areas, as to make defense of a fixed area both impracticable and energetically uneconomical. In many promiscuous species, males, by defending a predictable, localized, concentrated, and limited resource, can depend on being able to attract and to copulate with females. In contrast, a territorial, unmated male Comb Duck presumably has a relatively low chance of attracting a female. Intraseasonal variation in rainfall results in poor predictability of habitat quality, which may be one of the factors influencing the security of fixed-site tenure and the non-adaptiveness of "classical" territorial behavior. However, it is more relevant to identify the resources that a male Comb Duck might defend. There are three: nest sites, food, and females. The male does not defend the nest site. Food apparently is abundant and, probably more important, is renewed rapidly. Thus, current food levels are no guide to future food levels. The faster the rate of food replenishment, the more likely it is that the exploiter will find it advantageous not to exclude others from that resource and thereby not conserve the standing crop for its own future use. Defense of the female, on the other hand, is crucial. If the male defended an area with a fixed boundary, it is likely that the area required to sustain him and his female(s) would have to be larger than the area he actually defends. In attempting to exclude rival males from a relatively large defended area, the male would have to travel much farther, and possibly more often, than he actually does, thereby leaving his females exposed to rapists.

Since the quality of breeding habitat and mates varies, females must compete both directly and indirectly for those sets of resources which potentially facilitate the maximum return genetically. I assume that females compete directly for nest cavities and indirectly, by selecting the fittest males, for relatively superior feeding and brood-rearing opportunities. Males compete directly for females as mates, and for social and spatial positions facilitating optimum chances for encountering the fittest females. By acquiring and defending a mate, a breeding male enhances his opportunities for matings with supplementary females. Given suitable cavities nearby, these females are attracted to mate with such a male, because by doing so their reproductive success presumably will be higher than if they attempt to mate with an unmated male or mated male on poorer habitat.

Figure 4 is an incomplete arrangement of some of the presumed main relationships involved in the Comb Duck's social system. Further studies are needed to confirm these and other relationships. In particular, information is needed on reproductive success and survival rates of monogamous and polygynous females. Elliott (1975) has emphasized the role of longevity in the individual animal's total fitness in relation to the evolution of polygyny.

Summary

I studied the breeding behavior of the Comb Duck, *Sarkidiornis melanotus,* in southern Africa. Descriptions of displays and the social system are presented, and discussion focuses on factors which probably have acted in shaping the species' behavior. The Comb Duck has a repertoire of distinct displays, with clearly different signal postures used for aggression and courtship. The postures apparently have evolved in relation to the species' habit of spending much time perched in trees. Comb Ducks can be monogamous or polygynous, involving both harem and successive polygyny. Since quality of breeding habitat varies spatially and temporally, males compete with males, and females compete with females, both directly and indirectly, for those sets of resources which potentially will facilitate maximum genetic return. Females apparently compete directly for nest cavities and indirectly through fittest males for relatively superior feeding and brood-rearing opportunities. Males apparently compete directly for females as mates, and for social and spatial positions facilitating optimum chances for mating with fittest females.

Acknowledgments

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Immature Eastern Kingbirds, *Tyrannus tyrannus.* Painting by David Plank.

A REVIEW OF THE HORNBILLS: BIOLOGY AND RADIATION

ALAN C. KEMP

Hornbills, family Bucerotidae, with their bizarre bills and unusual breeding habits, have attracted considerable comment even though the majority of species remain to be studied in detail. In this review I will attempt to show the diversity of hornbill biologies that are indicated from the existing observations.

Male hornbills are slightly larger than females and the sexes can be distinguished by differences in plumage, bill, eye or facial skin colors, and often by the greater development of the casque atop the bill in males. Immatures may resemble either adult sex, show their true sex, or be quite different from adults, depending on the species. Vocal communications range from clucks through whistles to a variety or roaring, honking, and booming calls. Social organization varies from monogamous territorial species, through non-territorial communal feeding species, to those that exhibit group-territoriality and cooperative breeding. Most hornbills are omnivorous but some are carnivorous and others are frugivorous. Hornbills nest in natural holes in trees, rock faces, or earth banks. In most species the nest entrance is sealed up to a narrow vertical slit, the female remaining within and undergoing her flight-feather molt while being provisioned by the male. There is variation in which sex undertakes the sealing activity, when and how the female molts, which individuals provision the female and chicks, when the female emerges from the nest, and the skin color of the chick.

The external morphological characters and distributions of hornbills are well documented (Sanft 1960) and the behavioral and biological information will be reviewed. I will introduce the genera of hornbills and their constituent species in relation to their distribution and habitat preferences. The biology of each genus will then be considered in an attempt to synthesize the generic traits from the available evidence. The occurrence of mallophagan parasites will be mentioned. Finally I will discuss the relationships between the genera, which will summarize the generic traits and provide implications for discussion.

Distribution and Habitat Preferences

Forty-five species of hornbill in 14 genera (Sanft 1960) are distributed throughout the Ethiopian and Oriental Regions as well as peripherally in the Australasian Region (Table 1; Figure 1). There are 22 species in the Ethiopian Region, 19 in the Oriental Region, and four in the Australasian Region (east of Wallace's Line). The genus *Tockus* is the largest, with 14 species, and is the only genus with representatives in the Ethiopian and Oriental Regions; I suggest, however, that the oriental species deserve generic recognition (Kemp 1976). *Rhyticeros* (three species) and *Penelopides* (one species) are the only genera in the Australasian Region and both have most of their species in the Oriental Region. There are six monotypic genera, one in Africa and the rest in the Oriental Region.

Most hornbills inhabit forest (Figure 2), with only 11 species in savanna (nine *Tockus*, two *Bucorvus*), and three species on the forest edge *(Tockus, Bycanistes, Anthracoceros).* All but one savanna species are African, ranging from woodland to semidesert, with *Tockus monteiri* in the most arid habitat (Figure 3) of any hornbill (Kemp and Kemp 1972).

The Genera of Hornbills

I have tried to synthesize the essential biology of each genus from information on the species that have been studied, even though only rarely are all details for any one species known. Comments on the size proportions of hornbills are based on a series of measurements taken on each species.

Ethiopian *Tockus* Species

I began my work on hornbills by studying three *Tockus* species which coexisted in the savannas of southern Africa (Figure 4). Comparative observations on their ecology and behavior, followed by a study of a fourth species (Kemp and Kemp 1972), led to a systematic study of the whole genus (Kemp 1976). An important finding was that the species could be divided into terrestrial and arboreal foraging groups. Terrestrial foraging species have short wings, long tarsi, and utter clucking calls, whereas arboreal foraging species have long wings, short tarsi, and utter whistling calls (Kemp 1976). The largest genus, *Tockus*, also has four distinct groups of species among its African representatives, based mainly on their distinctive displays (Figure 2).

One group includes the Red-billed Hornbill *(T. erythrorhynchus)* and Monteiro's Hornbill *(T. monteiri)*. Short wings and a direct flight plus long tarsi support their terrestrial foraging. They utter clucking calls with the head bowed and the wings slightly opened during display (Figure 5Aa). Immature *erythrorhynchus* resemble adult males in bill color, but immature, male and female *monteiri* are separable in bill shape and facial skin color.

A second group includes the Yellow-billed Hornbill *(T. flavirostris)* and Von der Decken's Hornbill *(T. deckeni)*. Their short wings and long tails and tarsi are related to their direct flight and terrestrial foraging. The display consists of clucking calls uttered with the head bowed and the wings fanned over the back (Figure 5Ab, Figure 6). Immatures have dark bills that are retained in adult female *deckeni*, and the sexes differ in bill shape and color or the color of the facial skin. Most hornbills hop on the ground but the

Figure 1. The distribution of hornbill genera (after Sanft 1960). Small islands are only shown when they support hornbills: (1) *Tockus,* (2) *Anthracoceros,* (3) *Tropicranus,* (4) *Penelopides,* (5) *Ptilolaemus,* (6) *Bucorvus,* (7) *Buceros,* (8) *Anorrhinus,* (9) *Bycanistes,* (10) *Rhinoplax,* (11) *Berenicornis,* (12) *Ceratogymna,* (13) *Rhyticeros,* (14) *Aceros.*

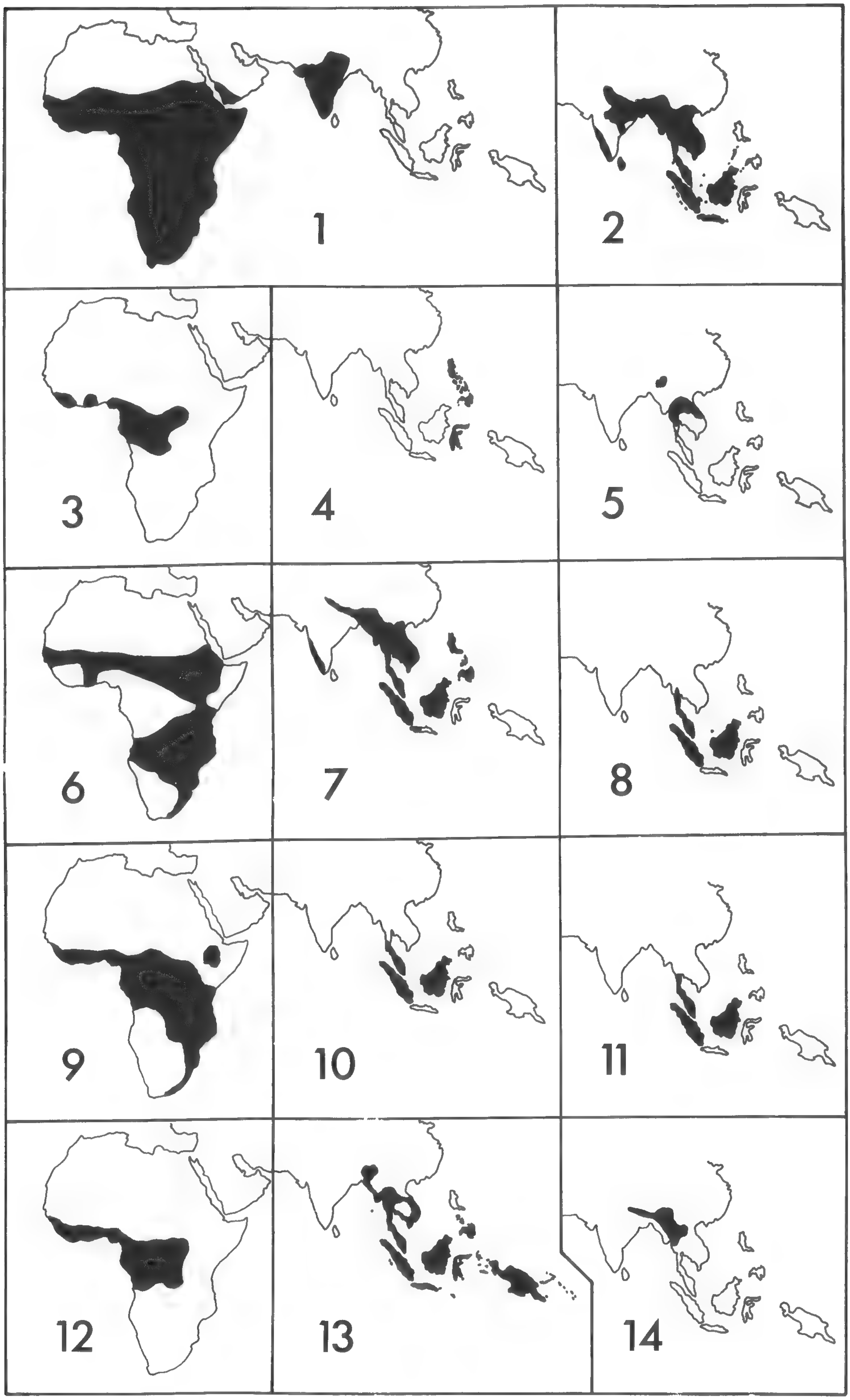
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TABLE 1

The Genera and Species of Hornbills (Sanft 1960)

Species	*Weight**	*General distribution and habitat*
Dwarf Black Hornbill *Tockus hartlaubi*	100	African lowland forest
Dwarf Red-billed Hornbill *Tockus camurus*	100	African lowland forest
Yellow-billed Hornbill *Tockus flavirostris*	200	Southern and eastern African savanna
Von der Decken's Hornbill *Tockus deckeni*	200	Eastern African savanna
Red-billed Hornbill *Tockus erythrorhynchus*	200	African tree and bush savanna
Monteiro's Hornbill *Tockus monteiri*	300	Southwest African savanna and steppe
African Grey Hornbill *Tockus nasutus*	200	African tree and bush savanna
Pale-billed Hornbill *Tockus pallidirostris*	200	Central African woodland
Hemprich's Hornbill *Tockus hemprichii*	300	African Abyssinian savanna
Bradfield's Hornbill *Tockus bradfieldi*	300	South-central African teak woodland
Crowned Hornbill *Tockus alboterminatus*	300	Eastern and southern African forest edge
African Pied Hornbill *Tockus fasciatus*	300	African lowland forest
Indian Grey Hornbill *Tockus birostris*	400	Indian savanna
Sri Lankan Grey Hornbill *Tockus griseus*	300	West Indian and Sri Lankan forest
Long-tailed Hornbill *Tropicranus albocristatus*	500	African lowland forest
Oriental Pied Hornbill *Anthracoceros coronatus*	1,000	Forest and forest edge of Asian mainland, Borneo, Sumatra, and Java
Palawan Hornbill *Anthracoceros marchei*	800	Palawan Archipelago forest
Sulu Hornbill *Anthracoceros montani*	800	Sulu Archipelago forest
Malay Black Hornbill *Anthracoceros malayanus*	1,000	Forests of Borneo, Sumatra, and Malay peninsula
Brown-backed Hornbill *Ptilolaemus tickelli*	900	Forests of southern Asian mainland
Bushy-crested Hornbill *Anorrhinus galeritus*	900	Forests of Borneo, Sumatra, and Malay peninsula
White-crested Hornbill *Berenicornis comatus*	1,700	Forests of Borneo, Sumatra, and Malay peninsula
Philippine Tacictic Hornbill *Penelopides panini*	500	Philippine forest
Celebes Tarictic Hornbill *Penelopides exarhatus*	500	Celebes forest
White-headed Hornbill *Rhyticeros leucocephalus*	1,600	Philippine forest

Species	*Weight**	*General distribution and habitat*
Wrinkled Hornbill *Rhyticeros corrugatus*	1,600	Forests of Borneo, Sumatra, and Malay peninsula
Celebes Hornbill *Rhyticeros cassidix*	2,400	Celebes forests
New Guinea Hornbill *Rhyticeros plicatus*	1,900	Forests of New Guinea Archipelago
Wreathed Hornbill *Rhyticeros undulatus*	2,500	Bengal and Assam forests south to Borneo and Java
Narcondam Hornbill *Rhyticeros narcondami*	500	Forests of Narcondam Island
Sumba Hornbill *Rhyticeros everetti*	600	Forests of Sumba Island
Rufous-necked Hornbill *Aceros nipalensis*	2,500	Forest from Himalayan foothills to Siam
Philippine Brown Hornbill *Buceros hydrocorax*	2,200	Philippine forests
Rhinoceros Hornbill *Buceros rhinoceros*	2,600	Forests of Borneo, Sumatra, Java, and Malay peninsula
Great Hornbill *Buceros bicornis*	3,000	West Indian forest and from Himalayan foothills south to Sumatra
Helmeted Hornbill *Rhinoplax vigil*	3,100	Forests of Borneo, Sumatra, and Malay peninsula
Abyssinian Ground Hornbill *Bucorvus abyssinicus*	4,000	African savanna north of the equator
Southern Ground Hornbill *Bucorvus leadbeateri*	4,000	African savanna south of the equator
Piping Hornbill *Bycanistes fistulator*	500	African lowland forest
Trumpeter Hornbill *Bycanistes bucinator*	700	Eastern African forest edges
White-thighed Hornbill *Bycanistes cylindricus*	1,300	African lowland forest
Brown-cheeked Hornbill *Bycanistes subcylindricus*	1,300	African lowland forest
Silvery-cheeked Hornbill *Bycanistes brevis*	1,300	Eastern African and Abyssinian montane forest
Yellow-casqued Hornbill *Ceratogymna elata*	2,100	Western African lowland forest
Black-casqued Hornbill *Ceratogymna atrata*	2,100	African lowland forest

*Estimated weight to the nearest one hundred grams.

species in these two groups walk, except for *monteiri*, whose bounds may be adaptive to its rocky habitat (Kemp and Kemp 1972).

The two species in the third group are the Pale-billed Hornbill *(T. pallidirostris)* and the African Grey Hornbill *(T. nasutus)*. Their long wings relate to their buoyant flight and arboreal foraging. Their whistled calls are given during display with the bill pointing up and the wings flicking (Figure 5Bc). Immature *nasutus* resemble adult males and the sexes differ in bill shape and color. In *pallidirostris*, ages and sexes are distinguishable by bill shape.

The last grouping of African *Tockus* hornbills includes Hemprich's

Figure 2. Tropical rainforest is the habitat of three-quarters of all hornbill species. This tract in the Gunong Mulu National Park, Sarawak, was inhabited by six species of hornbills.

Hornbill *(T. hemprichii)*, Crowned Hornbill *(T. alboterminatus)*, Bradfield's Hornbill *(T. bradfieldi)*, and African Pied Hornbill *(T. fasciatus)*. They, too, have long wings and short tarsi associated with arboreal foraging. They utter whistling calls with the bill pointed up (Figure 5Ba), except that *hemprichii* elaborates on this by fanning the tail over the back at the end of calling (Figure 5Bb). Immatures are distinguishable by bill shape and the sexes by facial skin color and bill shape.

The two remaining African hornbills of this genus are the smallest hornbills, restricted to forest and poorly known. The Dwarf Black Hornbill *(T. hartlaubi)* and the Dwarf Red-billed Hornbill *(T. camurus)* have short, narrow wings but *camurus* has long tarsi and forages on the forest floor, often following army ant columns, while *hartlaubi* has short tarsi and forages arboreally. The sexes differ in bill color and shape; but immature *hartlaubi* resemble the female while immature *camurus* resemble the male.

All species are omnivorous, but feed mainly on arthropods. In the three species I studied in detail, *nasutus, erythrorhynchus,* and *flavirostris*, representatives of 72 families of arthropods, mainly grasshoppers, beetles, ants, and termites, as well as snails, frogs, chameleons, mice, and 52 different fruits and flowers were recorded as food items. There was considerble overlap in diet, especially between the terrestrial foraging *erythrorhynchus* and *flavirostris*, but each species found its food in different places or obtained it in different ways. *T. nasutus* foraged arboreally, picking much of its food but also using its dextrous flight to pluck, hawk, and swoop after some. *T. erythrorhynchus* occurred mainly in areas with sparse grass cover and obtained much food by digging, especially during the dry winter when food was least abundant. *T. flavirostris* was least specialized in habitat requirements and foraging methods, other than finding most food close to ground level (Figure 7; Kemp 1976). *T. monteiri*, studied only during the breeding season, also ate a variety of food, especially large crickets and, like *erythrorhynchus*, dug for much of its food (Kemp and Kemp 1972).

Territories are formed with pairs showing their distinctive displays and defending their borders from neighbors. Territories of the arboreal foraging *nasutus* averaged 63 hectares, compared to 10 ha for *erythrorhynchus* and 17 ha for *flavirostris*, which forage terrestrially. Pairs examine potential nest holes from ground level up to over ten meters, but since holes are often used in successive years this often is not a prolonged activity. Regular interchange of nest holes between species occurs, but no interspecific territoriality has been recorded. All species appear to have similar hole requirements, typically with an entrance as small as possible and often less than 3 centimeters wide, the floor of the nest about 10 cm below the entrance, and a long chimney, or funkhole, above the nest into which the inmates can escape if the nest is broken into. These nest characteristics seem to apply to virtually all hornbill species, but obviously with variation in the dimensions. The location of the nest does not appear to be critical, since the entrance is sealed to form a narrow vertical slit through which predators rarely penetrate (Kemp 1971). The sealing is done by the female alone, initially with mud from the outside (Figure 8), and finally with her own droppings applied from within. Only in

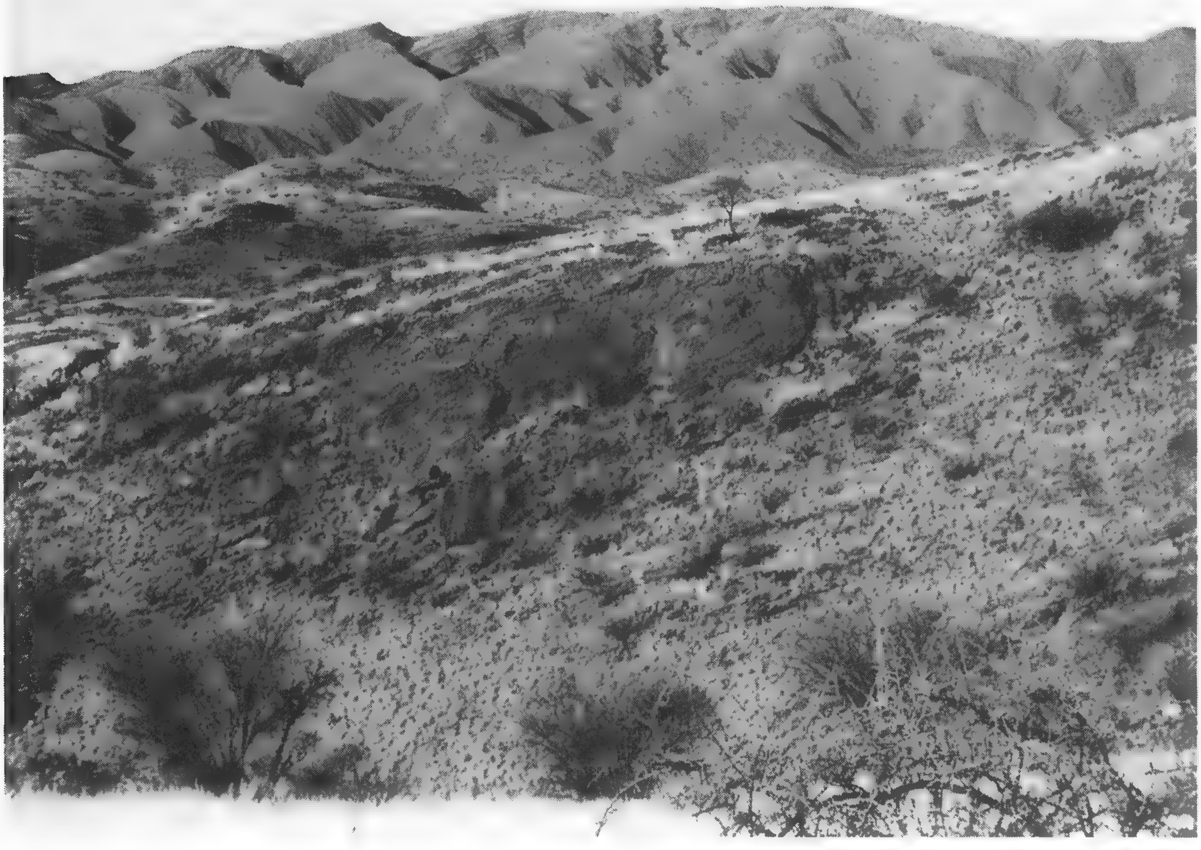


Figure 3. The arid habitat bordering the Namib Desert in South West Africa is the habitat of Monteiro's Hornbill, *Tockus monteiri*.

monteiri has the male been recorded assisting the female by bringing her mud in the end of his bill (Kemp and Kemp 1972).

The breeding female undergoes a simultaneous flight-feather molt which commences with the laying of the clutch of up to seven eggs. The female spends several days sealed into the nest before beginning to lay, losing the rectrices within a day of laying the first egg and usually dropping the remiges on the following day. Non-breeding hornbills have a normal sequential molt. The eggs are white, elongate ovals with a pitted shell, typical of all hornbills. Females lay eggs daily, and incubation begins with the laying of the first egg.

Incubation takes about 25 days, the chicks hatching at intervals of up to two days. The chicks retain a pink skin until feathering. When the chicks are about 20 days old, the female breaks out of the nest and the barely feathered chicks reseal the entrance alone using their own droppings (Figure 9). The chicks then remain in the nest for an additional 25 days, then break out and fly off, never to return to their nest. Throughout the incubation and early nestling periods, the male provisions the nest inmates with food carried as single items in the bill tip, with up to 10 feedings per hour being recorded (Figure 10). Once the female emerges, she assists in provisioning the chicks, whose feedings may rise to 16 items per hour. *T. monteiri* sometimes carries several items in the bill tip at once, but this is not perfected, since items are frequently dropped during transfer at the nest, and may be a partly developed adaptation to the dry habitat (Kemp and Kemp 1972).

The sealed-in nesting method appears to be very successful in preventing predation with over 90 percent of nests rearing some young to fledging (Kemp 1971). Food supply to the nest appears to be the main limiting factor that determines clutch size and the survival of the younger members of broods. Other factors also affecting breeding success are death of the male parent, flooding of the nest hole, and tree growth rendering the entrance

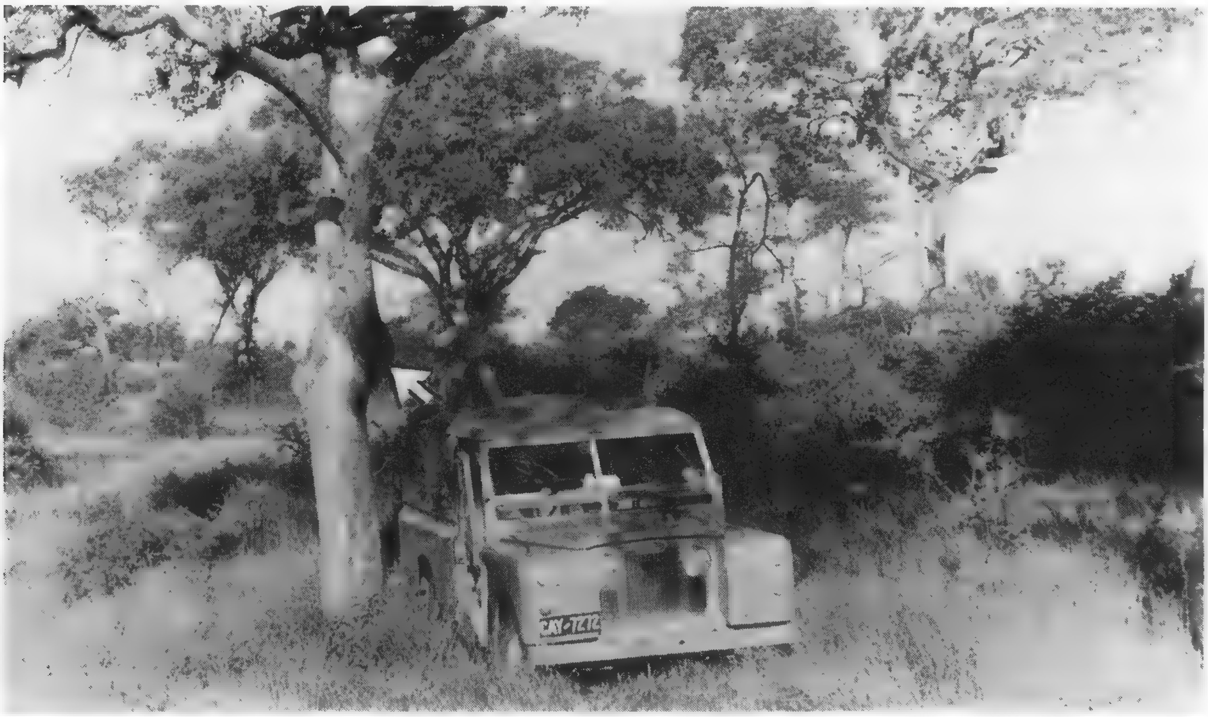


Figure 4. The habitat in which three species of *Tockus* hornbills coexisted in the central Kruger National Park, Republic of South Africa. The observers point to simultaneously active nests of two species in the same tree, *T. flavirostris* in the trunk and *T. erythrorhynchus* in the branches.

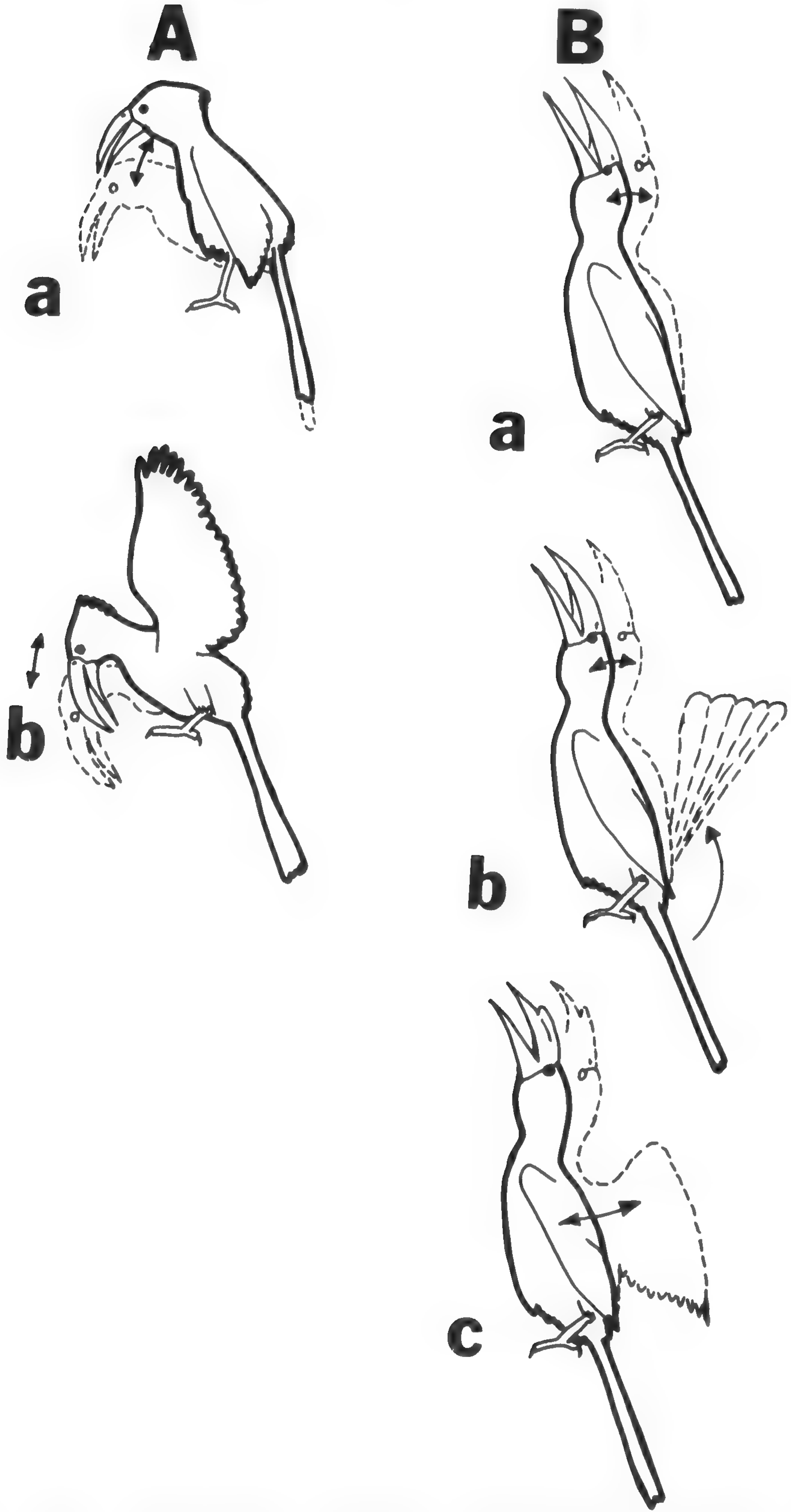


Figure 5. Diagrammatic illustration of the displays of *Tockus* species: A—terrestrial foraging species which utter clucking calls; B—arboreal foraging species which utter whistling calls. See text for further details.

hole too small for the inmates to emerge (Kemp 1971, 1976; Kemp and Kemp 1972).

Tropicranus

The Long-crested Hornbill *(T. albocristatus)* has the proportions of a large arboreal foraging *Tockus* species except for the long graduated tail, and I suggest that they are congeneric. Immature *Tropicranus* differ from adults in eye color and the sexes are differentiated by bill shape. *Tropicranus* is a little-known African forest species that is omnivorous, although mainly insectivorous, foraging just below the canopy and apparently often following monkey troops for the insects they disturb (Cahpin 1939). Like African *Tockus* species, *Tropicranus* takes single items of food to the nest in the bill, has chicks with pink skin, molts the flight feathers simultaneously when breeding, and is monogamous.

Oriental *Tockus* Species

I have indicated elsewhere that these two species deserve generic separation from the African members of *Tockus* (Kemp 1976). They differ in aspects of plumage, flight, lack of displays, calls, and in feeding at the nest by regurgitation of food items. The Indian Grey Hornbill *(T. birostris)* superficially resembles the African *nasutus* in bill shape and whistling calls, but differs in having short wings, a direct parrot-like flight unique within the family, and a long tail accentuated by elongated central rectrices. Immatures differ from adults in their bill color and the sexes differ in the shape of the casque. The species occurs in small parties and apparently breeds

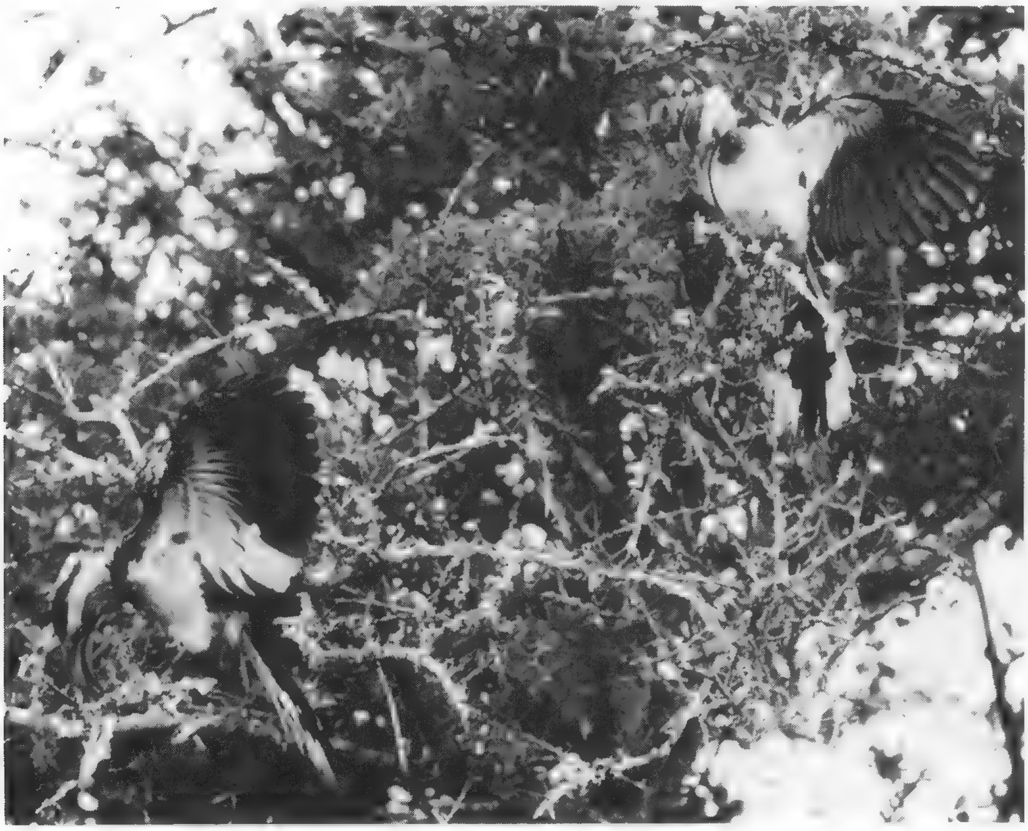


Figure 6. A pair of Yellow-billed Hornbills, *Tockus flavirostris,* displaying with the head bowed down to the feet and the wings fanned over the back, accompanied by a crescendo of clucking calls.

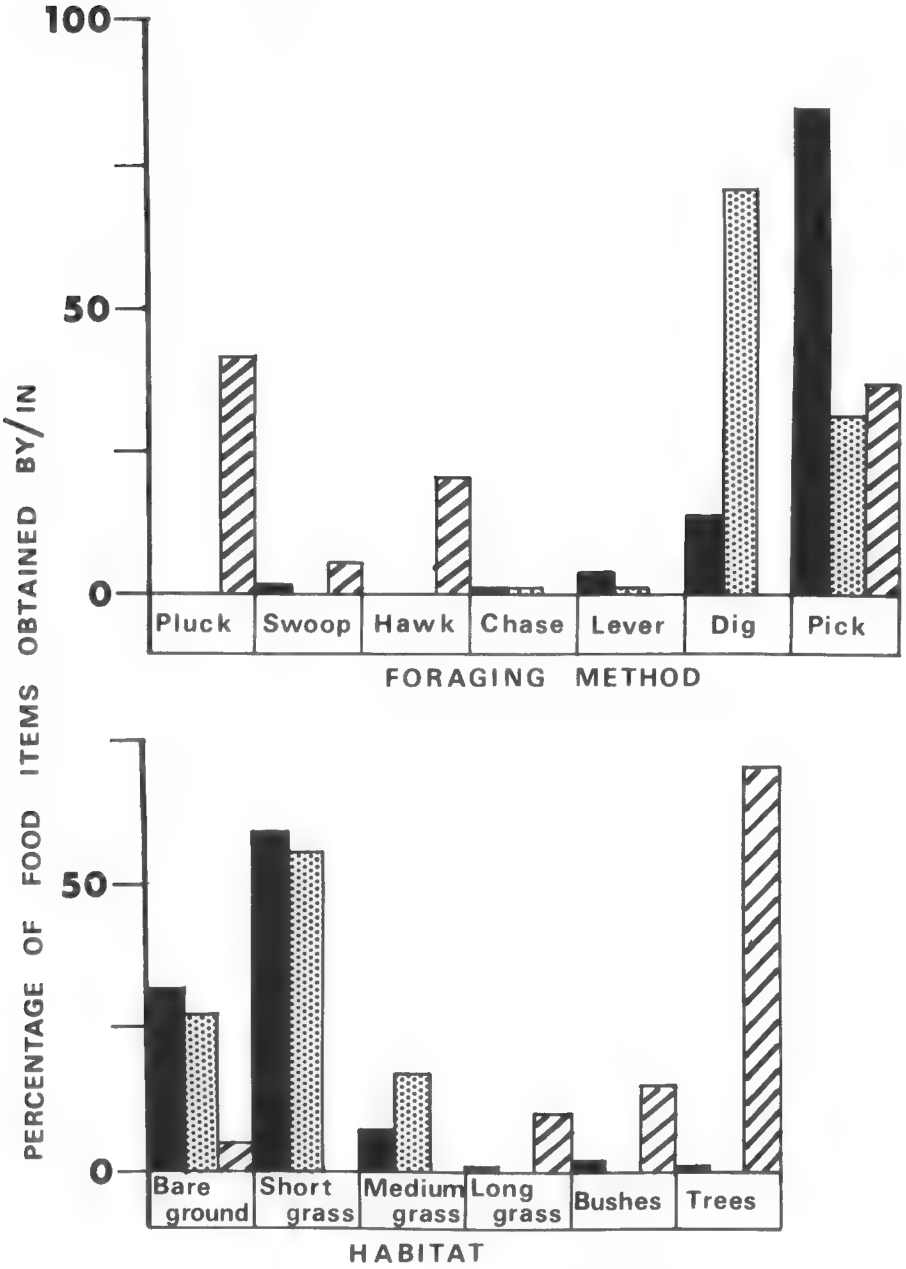
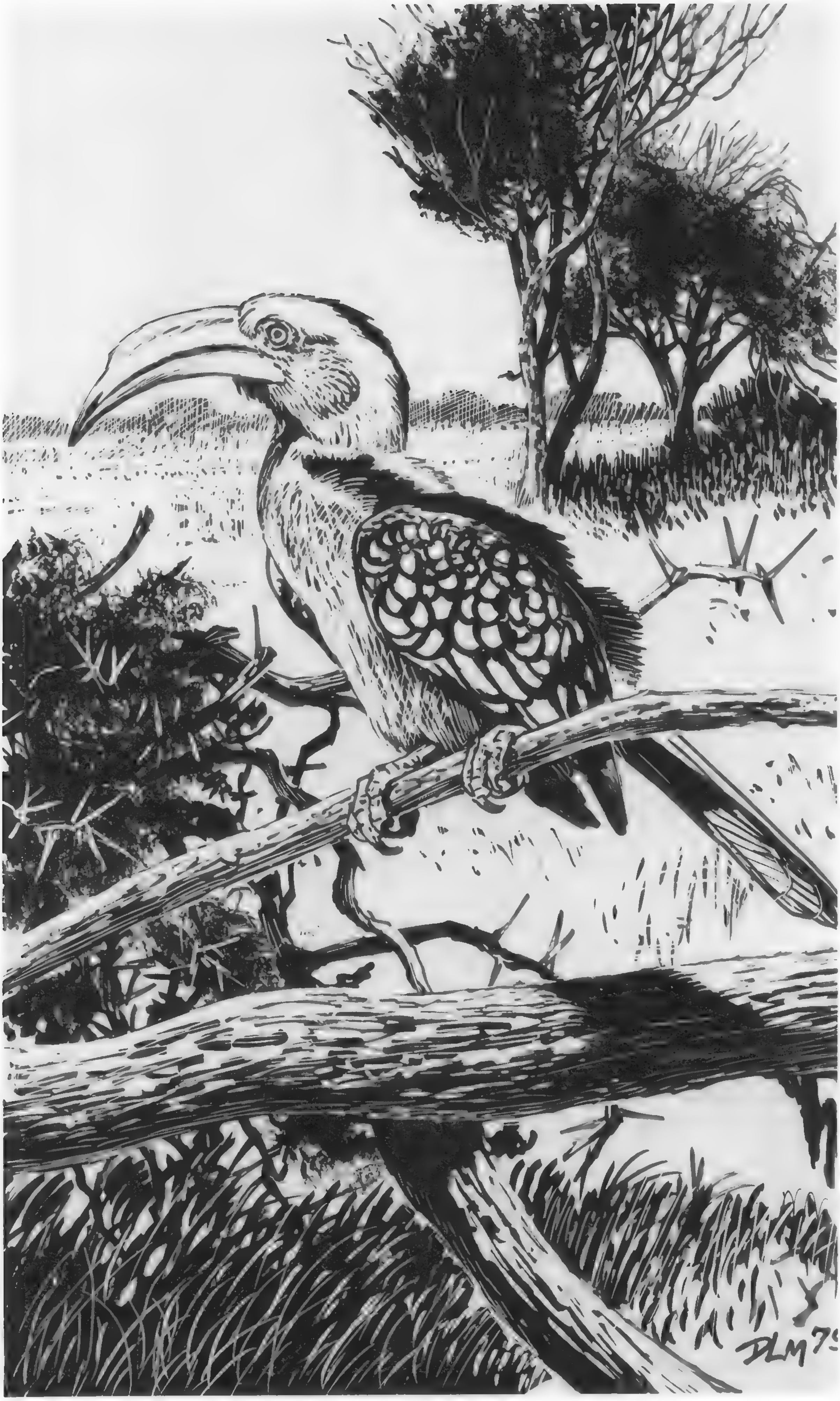


Figure 7. How, and in what habitat, three species of *Tockus* hornbills obtained their food during the dry season (May to October) when food was least abundant and each species exhibited its foraging specializations (after Kemp 1976). Solid bars—Yellow-billed Hornbill, *T. flavirostris*; stippled bars—Red-billed Hornbill, *T. erythrorhynchus*; hatched bars—African Gray Hornbill, *T. nasutus*.

monogamously, but nests are close together (Hall 1918) with more than a pair in attendance (Horne 1869); and the separate immature coloration suggests that cooperative breeding may occur.

The second species, the Malabar Grey Hornbill *(T. griseus)*, has distinct Indian and Sri Lankan populations that probably deserve specific status. The two populations differ notably in bill, head, and tail coloration. In the nominate Indian race, the immatures are colored like adult males, while in the Sri Lankan *T. g. gingalensis* they differ from both adults. Both populations have clucking and whistling calls unlike any other member of the genus. Nominate *griseus* occurs in small parties and is reported to breed monogamously, but the distinct immature coloration of *gingalensis* suggests cooperative breeding.

In most respects the oriental *Tockus* species resemble the African species in their biology. They feed on a wide range of foods including much fruit but also on such items as lizards and bird eggs (Lowther 1942). When breeding,



Yellow-billed Hornbill, *Tockus flavirostris.* Drawing by Donald Malick.

the female seals herself into the nest, although a male *birostris* has been reported to bring sealing material to the female (Hall 1918). The breeding female undergoes a simultaneous flight-feather molt (Abdulali 1951; Findlay 1928; Horne 1869). Up to four eggs may form the clutch (Ali and Ripley 1970). Food is mostly regurgitated to the nest inmates, although occasionally it is brought as a single item in the bill (Lowther 1942; Punchihewa 1968). The chicks have pink skin and the female breaks out when the chicks are at least one third grown. The nesting cycle is of similar duration to the African *Tockus* species.

Anthracoceros

This genus probably consists of a superspecies plus two other rather different species that may not be congeneric. The widespread Oriental Pied Hornbill *(A. coronatus)* should probably be considered as two species in a superspecies with the Palawan Hornbill *(A. marchei)*. Nominate Indian *coronatus* has pink throat skin and extensive white in the underparts and tail. Further east *A. c. albirostris* and *A. c. convexus* have white throat skin and reduced white plumage areas; and finally *marchei* has white throat skin, black underparts, and a white tail. All members of the superspecies have very similar whistling and cackling calls (Ali and Ripley 1970; Clifford Frith, pers. commun.). Adults and immatures differ only in bill shape. The Malay Black Hornbill *(A. malayanus)* has elongated central rectrices and deep growling calls, and the sexes differ in bill color with immatures resembling males (Smythies 1968). The sexes of the Sulu Hornbill *(A. montani)* differ in eye color, but immatures and calls of this species have never been described.

All species in this genus reportedly move in pairs or small parties and rarely congregate at food sources. They are probably territorial and monogamous when breeding. The breeding of *marchei* and *montani* is undescribed. In *malayanus* and *coronatus* the nest entrance is sealed, the male of the latter bringing sealing material to the female in his bill (Bartels and Bartels 1937; Hutchins 1976). The female appears to undergo a simultaneous flight-feather molt while breeding *(A. c. albirostris*, Hutchins 1976). *A. malayanus* lays up to three eggs but only nests with single chicks have been reported (Kemp and Kemp 1975). *A. coronatus* lays up to four eggs with several chicks being reared. Both species are omnivorous and forage in tangled, often secondary forest, with *coronatus* extending from the forest edge into parkland in search of food. Species of this genus feed on fruits and any animals they encounter such as insects, lizards, and snakes, as well as robbing nests of small birds, hawking termites, and even catching fish (Kemp and Kemp 1975; Lowther 1942). The food is regurgitated to the nest inmates, but in *malayanus* the male often brings single items in the bill (Bartels and Bartels 1937). The skin color of chicks is pink in *coronatus* (Clifford Frith, Elliott McClure, pers. commun.) and pinkish yellow in *malayanus* (Elliott McClure, pers. commun.). *A. c. coronatus* females have twice been noted to leave the nest when the chicks were about half-grown (Lowther 1942). However, a captive *A. c. albirostris* female only left after the departure of her two chicks (Hutchins 1976), and a female *malayanus* in the nest with a large chick indicates a similar pattern for this species (Kemp and Kemp 1975).

Ptilolaemus

The Brown-backed Hornbill *(P. tickelli)* has been little studied. The sexes

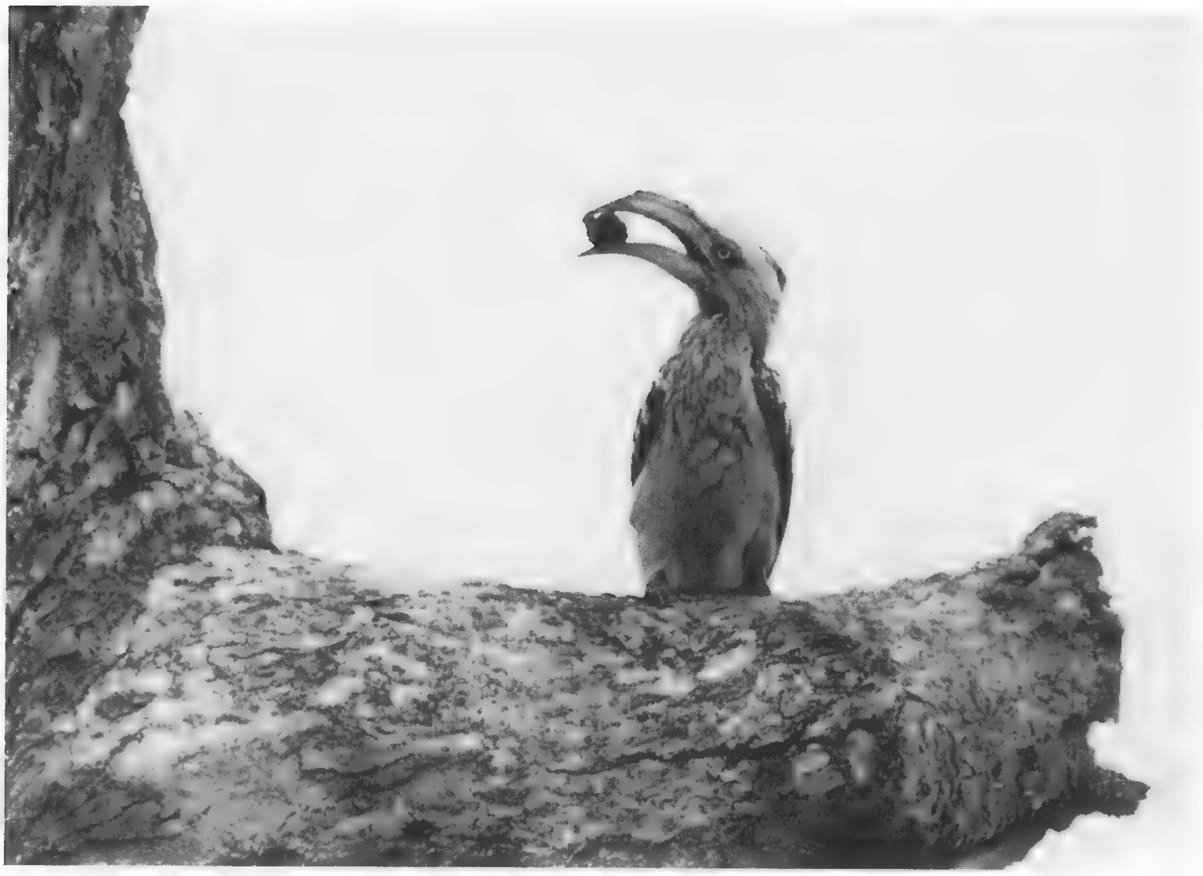


Figure 8. A female Yellow-billed Hornbill, *Tockus flavirostris*, with mud she had collected at the base of the nest tree and which is to be used in preliminary sealing of the nest entrance.

differ in bill color and immatures resemble adult males. The species is reported to be noisy, with various whistling calls, and to occur in small flocks (Tickell 1864). Stomach contents indicate an omnivorous diet (Sanft 1960). The immature plumage coloration suggests that the species is a monogamous breeder. Nest entrances are sealed, apparently by both sexes, with the male supplying mud and the female applying it (Bingham 1879). Up to five eggs are laid and the chicks have cream-colored skin (Elliott McClure, pers. commun.).

Anorrhinus

The Bushy-crested Hornbill *(A. galeritus)* is similar in size and bill shape to *Ptilolaemus*, but with longer wings that provide buoyant flight. The sexes are differentiated by bill color, but immatures differ from adults in both bill and facial skin colors. This noisy species has a variety of whistling calls. It is social and definitely group-territorial, with usually up to ten birds in a group but up to 20 being recorded (Kemp and Kemp 1975). In Sarawak, groups occupied about 200 ha of forest. The group breeds cooperatively, with all ages and sexes bringing food to the single female in the nest (Kemp and Kemp 1975; Madge 1969; Sharpe 1890). Food — mainly fruits, but also cockroaches, lizards, and cicadas—is regurgitated to the nest inmates. *Anorrhinus* forages largely below the canopy, often down to ground level, and seems to favor dense tangled growth.

The nest is sealed but the roles of the sexes in sealing are unknown. The breeding female apparently undergoes a simultaneous flight-feather molt (Sharpe 1890) and emerges with the chicks at the end of the nesting cycle.

Only two chicks have been recorded in a brood and this probably indicates the normal clutch (Kemp and Kemp 1975; Madge 1969). The chicks have pinkish yellow skin (Elliott McClure, pers. commun.). The nesting cycle takes at least 10, and probably 12, weeks. More than one nesting attempt may occur per year, with as little as two weeks between cycles. Therefore, no definite breeding season is apparent (Madge 1969). It is not known if the same female in the group breeds on each attempt.

Berenicornis

The White-crested Hornbill *(B. comatus)* is a striking pied bird, with rather short wings and a long tail resulting in direct flight. The white tail is conspicuous in flight and the white crest when at rest, while the soft hooting calls often reveal this secretive species. The sexes differ, males having white head and breast while only the crest is white in females. Immatures differ completely from both adults in bill and plumage color. The species usually occurs in groups of four to six, with up to 20 being recorded. The groups are definitely territorial in Sarawak (Kemp and Kemp 1975). They occur in large areas of dense tangled growth, foraging slowly and systematically through the subcanopy, even close to the ground. They may be more carnivorous than most larger forest hornbills, with birds and lizards reported in their diet (Kemp and Kemp 1975). They have been seen examining active woodpecker holes (Lester Short, pers. commun.).

The immature coloration and social organization suggest that the species breeds cooperatively, although details are lacking. Nests reportedly are sealed and contain a single chick (Dunselman 1937; Smythies 1968); but twice two chicks of similar age were brought to the Bangkok market Clifford Frith, pers. commun.), indicating that two eggs may be laid.

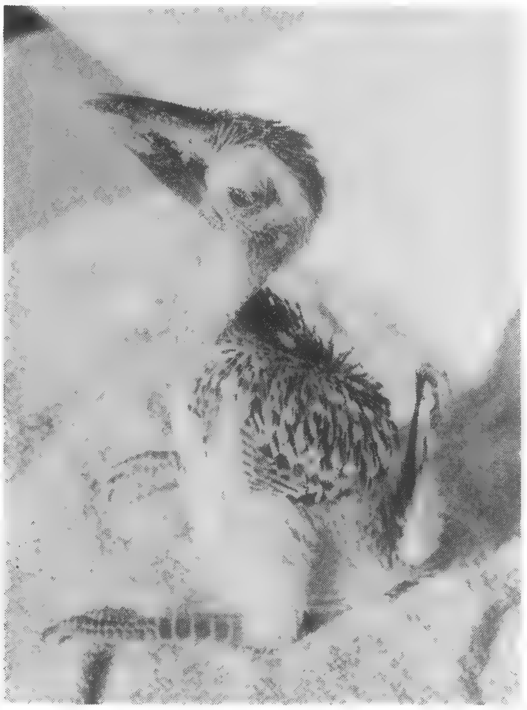


Figure 9. A 20-day-old Yellow-billed Hornbill, *Tockus flavirostris*, chick which had just completed resealing itself into a nest hole after the emergence of the female. Note the position in which the tail is held in the nest.

Penelopides

Very little is known of this genus. The Philippine Tarictic Hornbill *(P. panini)* is probably a superspecies complex of four species, from which the Celebes Tarictic Hornbill *(P. exarhatus)* is clearly separable. In all species the males have white heads, while the females have black or brown, except for *P. p. mindorensis* in which the sexes are identical. Immatures of both sexes resemble adult males in *exarhatus*, nominate *panini*, and *P. p. ticaensis*, but show their true sex in other races of *panini* except for *mindorensis.*

Nothing is known of the biology of these species other than that they occur in small parties and utter loud squeaking calls like those of *Anorrhinus* (Clifford Frith, pers. commun.; Derek A. Holmes, tape recording). A captive female sealed the nest with little assistance from the male (Jennings and Rudel 1976). Female *panini* molt their flight feathers while breeding and reportedly lay up to four eggs in a clutch (McGregor 1905). A captive female emerged with the single chick at the end of a 102-day nesting cycle, and two weeks later began nesting again.

Rhyticeros and *Aceros*

Seven species of *Rhyticeros* and monotypic *Aceros* are spread throughout the Oriental Region and into the Australasian Region. Where they occur sympatrically they exhibit differences in size, proportions, and biology. The Rufous-necked Hornbill *(A. nipalensis)* has a long bill. The Wrinkled Hornbill *(R. corrugatus)* and White-headed Hornbill *(R. leucocephalus)* have wrinkled, upright casques and short wings, tail, and tarsi. The other five *Rhyticeros* species have long broad wings, with short tails in all but the insular Sumba Hornbill *(R. everetti)*. They have flattened, wreathed casques in all but the Celebes Hornbill *(R. cassidix)*, which has a laterally-compressed ridge for the casque. All are rather large species except for the insular *everetti* and Narcondam Hornbill *(R. narcondami)*. In all species immatures and adult males have a brown and/or white head and neck; these areas are black in females. The Weathered Hornbill *(R. undulatus), corrugatus,* and *leucocephalus* have white tail feathers that are stained yellow, apparently with preen gland oil (Harrison 1963). The bare throat is inflated in adult *undulatus, narcondami,* and *corrugatus*, and probably also in the New Guinea Hornbill *(R. plicatus)* and *Aceros*.

Calls, where known, are always repeated barking notes: *corrugatus* and *undulatus* (Kemp and Kemp 1975), *narcondami* (S. Hussein, pers. commun.), *plicatus* (Gilliard and LeCroy 1967), and *Aceros* (Ali and Ripley 1970). *R. undulatus* and *narcondami* jerk the bill upward with each note when they call from a perch, but not *corrugatus*. In *Aceros* the calling consists of roars and barks, sometimes with a pair in duet, bill skyward, head feathers raised, and the tail jerked up to touch the back of the head at the climax (Ali and Ripley 1970).

Where food habits are known, the species are omnivorous and possibly more carnivorous while breeding (Bartels 1956). They feed on fruits, including many figs, and the animal food includes bats, reptiles, frogs, crabs, and insects. In Sarawak, *corrugatus* was found to be sedentary and in smaller groups than *undulatus* (Kemp and Kemp 1975). It forages mainly above the canopy, even plucking insects from the foliage in flight. Flocks of up to 20 birds have been recorded (Harrison 1963).

R. undulatus has much greater spatial requirements, flocks of 20 being

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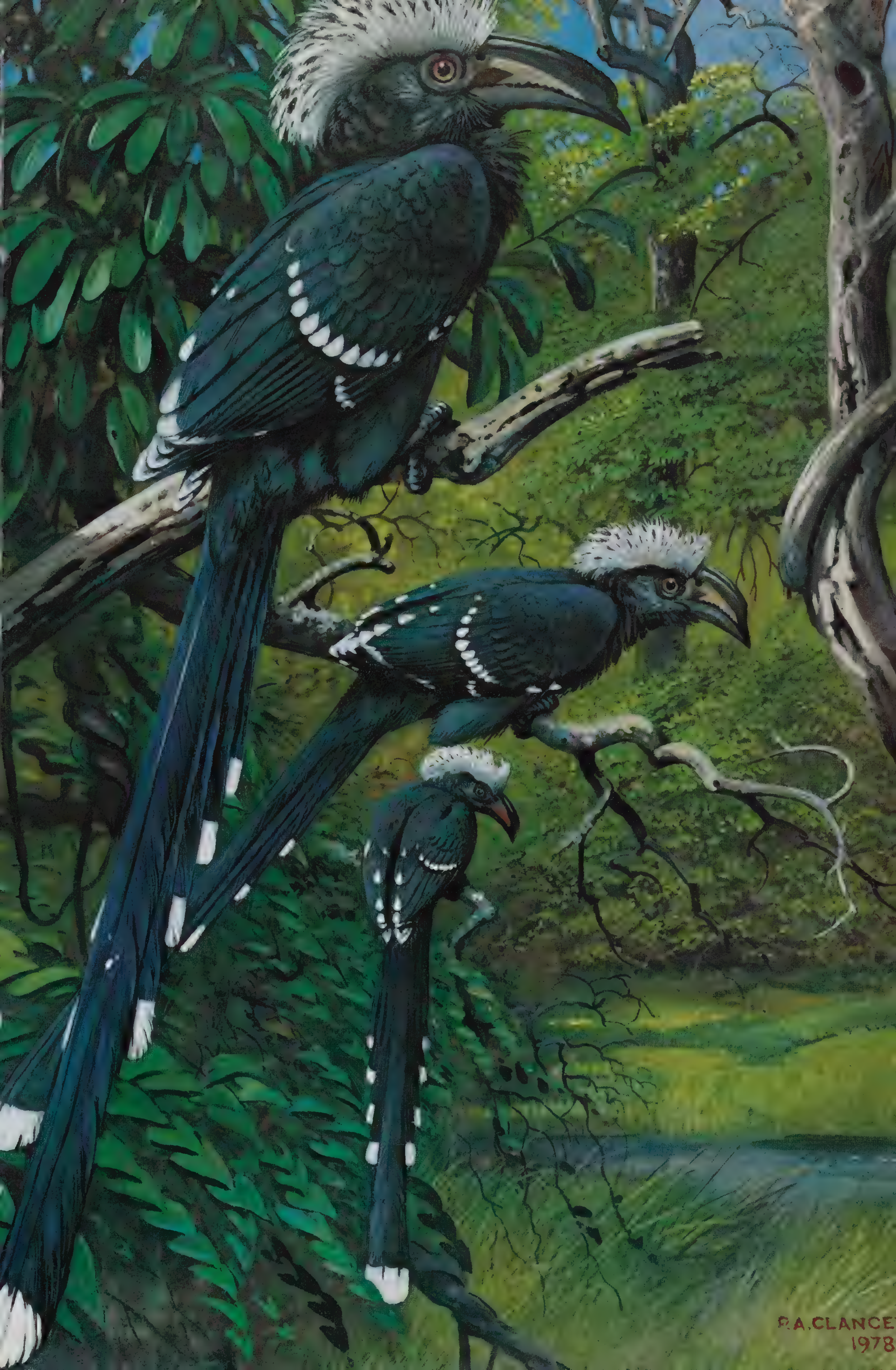
Long-tailed Hornbill, *Tropicranus albocristatus*. Painting by P. A. Clancey.


P.A. CLANCEY
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regular with many more congregating at feeding and resting sites. Flocks range far in flight, up to seven kilometers in one flight and even crossing the sea to offshore islands (Anderson 1887; Kemp and Kemp 1975; Tickell 1864). Dropping down in response to calls or when spotting others below, they congregate at feeding and bathing sites, with up to 400 at communal roosts (Kemp and Kemp 1975; McClure 1964, 1970; Tickell 1864). *R. undulatus* is a generalized forager, from the canopy to the forest floor, and even in water (Kemp and Kemp 1975; Tickell 1864), feeding singly or communally and exhibiting catholic tastes. *R. leucocephalus*, with similar proportions to *corrugatus*, probably resembles that species in its biology, and other *Rhyticeros* may resemble *undulatus*. *Aceros* is sedentary and feeds at all levels in the forest (Ali and Ripley 1970).

All species are monogamous where breeding has been observed. The breeding of *undulatus* is well known (Bartels 1956), but the nests of the other species are little studied and those of *everetti* and *leucocephalus* remain undescribed. In *undulatus* the pair begin to visit the nest up to two months before laying, using the same nest hole in a forest tree for as long as nine successive years. Typically the entrance hole is just large enough to admit the female, and is sealed by the female alone. Incubation takes about five to six weeks, but the whole nesting cycle takes four and a half months, with the female emerging with a single chick at the end of the cycle.

A female *undulatus* taken from a nest appeared to have undergone a simultaneous flight-feather molt (Bernstein 1861) and although this has been discounted (Bartels and Bartels 1937), only a female at the end of the nesting cycle was examined. *Aceros* also appears to undergo a flight-feather molt while breeding (Gammie 1875). Food is regurgitated to the nest inmates by the male. Females lay as many as three eggs but usually rear only one young. The younger chicks probably die of starvation as in *undulatus* (Bartels and Bartels 1937). However, the small *narcondami* can raise two young (Ali and Ripley 1970; S. Hussein, pers. commun.). The chicks of *undulatus* have deep purple body skin (Coenraad-Uhlig 1930; Clifford Frith, pers. commun.; Elliott McClure pers. commun.).

Buceros

The following three genera contain the largest hornbills. The Philippine Brown Hornbill *(B. hydrocorax)* has short and narrow wings, while the spectacular Great Hornbill *(B. bicornis)* and Rhinoceros Hornbill *(B. rhinoceros)* have long wings as well as long bills and large casques. The sexes differ in eye color and immatures differ from adults in eye color and development of the casque. In *hydrocorax* the immatures differ completely from the adult, being black and white instead of brown and black, having a black tail band instead of a pure white tail, and having a bill that is black instead of orange. All species have colored feet, which is unusual in the family where they are usually dark slate or black. The red and yellow coloration of the casque, the bill, and white plumage areas is cosmetic coloration from preen gland oils, applied with a special tuft of feathers around that organ. Immatures apparently do not have the colored preen gland oils. The main call of all species is a loud honking (Ali and Ripley 1970; Bartels and Bartels 1937; Stott 1947), usually as a duet in *rhinoceros* (Kemp and Kemp 1975), and sometimes giving way to roaring calls in *rhinoceros* and *bicornis,* with the bill pointing upward.

The biology of *hydrocorax* is little known. Its proportions indicate that it is

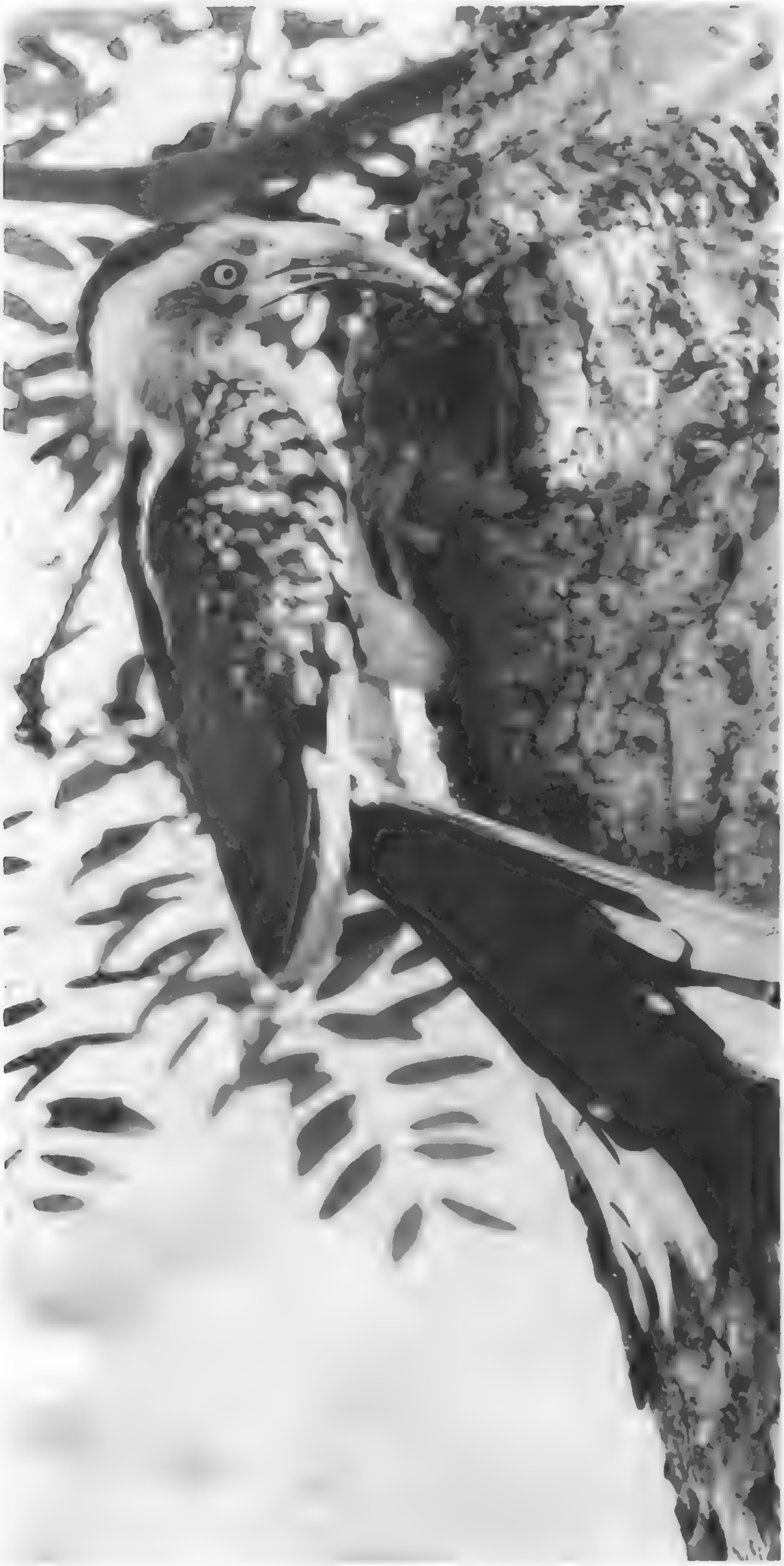


Figure 10. A male Red-billed hornbill, *Tockus erythrorhynchus*, presenting a single food item to a female at the nest entrance. Note the minimal size of the entrance hole.

sedentary, and the unique coloration of immatures suggests that this species breeds cooperatively. The Philippine Brown Hornbill is probably also group-territorial as it is normally observed in parties of three to seven birds (Stott 1947). *B. rhinoceros* and *bicornis* are monogamous when breeding, although more than one male *rhinoceros* has been recorded attending a nest (Shelford 1899). One regularly encounters both species in pairs, but they are sometimes seen in flocks of up to 17 for *rhinoceros* and over 100 for *bicornis* (Ali and Ripley 1970; McClure 1964, 1970). These species may be territorial when breeding, with nonbreeding birds forming into flocks. In parts of Sarawak, pairs of *rhinoceros* appeared to be maintaining territories as indicated by duetting and responding to playback of calls while elsewhere they occurred in flocks (Kemp and Kemp 1975). All species appear to be omnivorous, eating much fruit but also taking such animal food as they encounter, including frogs, lizards, birds, spiders, and various insects.

All species nest in holes in large forest trees, again with the entrance hole as small as possible. The male begins to courtship feed the female over a month before she enters the nest. The roles of the sexes in sealing the nest are unknown, although in captive *bicornis* both sexes participated (Poulsen 1970; Stott 1951). The female remains in the nest for about 90 days, during which the usual clutch of two eggs is laid, the chicks are hatched, and the single surviving chick is partly raised. The female then breaks out of the nest, leaving the chick to reseal the entrance. She helps to feed the chick for the remaining 40 days of the nestling period. The nest inmates are fed by regurgitation, with up to 22 fruits being brought in one load. The chick takes about four years to attain adult development of the casque and plumage. These observations on nesting pertain mainly to *rhinoceros* and *bicornis* (Ali and Ripley 1970; Bartels and Bartels 1937; Hetharia 1937). The female apparently undergoes a simultaneous flight-feather molt while in the nest (Tickell 1864). The chick of *bicornis* has a dark purplish pink skin (Clifford Frith, pers. commun.).

Rhinoplax

The striking Helmeted Hornbill *(R. vigil)* is probably an aberrant form of *Buceros*. The central pair of rectrices are greatly elongated and the blunt casque is unique in being of solid "ivory" in front so that the skull forms 10 percent of the body weight and is greatly reinforced (Manger Cats 1961). The feet are reddish brown, the casque and bill are colored with crimson oil from the preen gland secretions (Harrison 1951), and the tail has a black subterminal band as in *Buceros*. Both sexes have extensive areas of bare skin on the head and neck that differ only in the coloration on the throat. The bill in immatures is a light horn color and the casque and central tail feathers undeveloped. The species is unique within the family in that the central tail feathers are molted in succession (Wetmore 1915).

The main call, uttered by adults with females calling in a higher pitch than males, is an accelerating series of hoots ending in maniacal laughter. A roaring call is also uttered when in flight and when very excited, often with the bill pointing upward. *Rhinoplax* is highly territorial, responding to playback and imitation of its hooting call, a fact long known to Bornean hunters (Banks 1935; Kemp and Kemp 1975). Spatial requirements are of the order of 160 ha of primary forest per pair. Pairs or family parties are usually encountered, but a flock of eight has been recorded (Kemp and Kemp 1975) and numbers congregate at fruiting trees (Schneider 1945).

The vigilance of the species is not a misnomer, and little of the biology has been discovered. *R. vigil* is probably omnivorous, most stomachs of collected birds containing fruit but also the remains of birds and squirrels. The straight weighted bill is suspected to be for digging in rotten wood and tree holes, where the bare head and neck would also be advantageous.

Rhinoplax has been seen trying to break into the nest of a smaller hornbill (Bartels and Bartels 1937). The use of the bill as a dagger in fighting has twice been recorded (Schneider 1945) and parallels observations on fighting *Buceros rhinoceros* (Lord Medway, unpubl. notes). Possibly the casques of these large hornbills serve specialized feeding functions. The few nests of *Rhinoplax* that have been found were sealed and one contained a single chick. A female was in the nest with the large chick, indicating that she may only leave the nest at the end of the nesting cycle (Schneider 1945).

Bucorvus

The two ground hornbills are the largest and most aberrant of the family. They are adapted for a terrestrial existence in the African savanna and occur allopatrically on either side of the equator. They have long legs, short toes, broad wings, and 15 cervical vertebrae (one more than other hornbills). Apart from three *Tockus* species, they are the only hornbills that walk, doing so on the tips of their toes; and they are the only hornbills that scratch directly. They are black turkey-sized birds with white primaries, extensive areas of bare facial skin, and inflatable throats. The northern Abyssinian Ground Hornbill *(B. abyssinicus)* has a longer bill and cowl-like casque compared to the Southern Ground Hornbill *(B. leadbeateri)* which has a short bill and negligible casque (Figure 11). Adult sexes are separable by the colors of the bare facial skin, and immatures differ from adults in having pale gray skin areas, deflated throats, and gray bills. The feather tuft around the preen gland is developed as in *Buceros* and *Rhinoplax* even though no cosmetic coloration is evident in ground hornbills, except possibly the small yellow patch at the base of the bill in *abyssinicus*.

The calls are deep booming notes audible over distances up to 4.5 km, and are useful in proclaiming a territory that in *leadbeateri* is of the order of 100 km^2. Both species are almost entirely carnivorous (Kemp and Kemp 1977), taking a variety of foods as they walk steadily over the savanna. Much of the diet of *leadbeateri* consists of insects, especially grasshoppers and beetles, but snails, lizards, and snakes are also important and even hares and squirrels are captured at times. Both species are territorial and live in small groups, but apparently with different kinds of social organization (Kemp and Kemp, in press). *B. leadbeateri* is group-territorial and breeds cooperatively, with a mean group size of four or five birds and up to eight recorded. *B. abyssinicus* is usually recorded in pairs or small families and probably breeds monogamously. In addition, immature *leadbeateri* do not develop adult plumage and coloration until six years old, while *abyssinicus* attain adult plumage and soft part coloration even before a year old (Anonymous 1974).

Both species are unique among hornbills in not sealing the nest entrance. They may also be the only hornbills capable of excavating their own nest holes in earth banks (Kemp and Kemp, in press; Penny 1975). The breeding female does not undergo a simultaneous flight-feather molt while incubating the normal clutch of two eggs. Food, and the deep nest lining of leaf and grass, is carried to the nest in the bill tip, as a bolus of items rather than as single pieces. The female remains in the nest for the incubation period and early nestling stage despite not being sealed in, only emerging two or three times daily to defecate. Ground hornbills are also the only hornbills that do not effect nest sanitation by squirting out their droppings through the nest entrance. The breeding female is fed in the nest, in the case of *leadbeateri* by the whole territorial group, which makes about five visits to the nest daily. Incubation takes about 40 days, and even if both eggs hatch, the second chick dies of starvation since it hatches several days after the first and is too small to compete with its sibling (Kemp and Kemp, in press; Penny 1975). The skin of the chick changes from pink to dark purple a few days after hatching. The breeding female emerges for long periods to assist in feeding the chick when it is about one third of the way through its 86-day nestling period. The chick can fly well on emergence and, in the case of *leadbeateri*, remains dependent on the group for food for as long as two years before contributing to group activities at the nest.

Bycanistes

All five of these African species are pied and differ from other genera in having white rumps. The development of the casque in the males is the striking sexual character, with the casque also being differently colored in the male of the White-thighed Hornbill *(B. cylindricus)*, Brown-cheeked Hornbill *(B. subcylindricus)*, and Silvery-cheeked Hornbill *(B. brevis)*. Immatures resemble females in casque development and are separable in always having brown feathers on the forehead.

All species have distinctive loud calls, from the whistling of the Piping Hornbill *(B. fistulator)*, wails of the Trumpeter Hornbill *(B. bucinator)*, clucks

Figure 11. A small group of Southern Ground Hornbills, *Bucorvus leadbeateri,* during territorial calling. The female in the center utters the deep booming notes while the males on either side wait to perform their part of the duet in deeper tones.

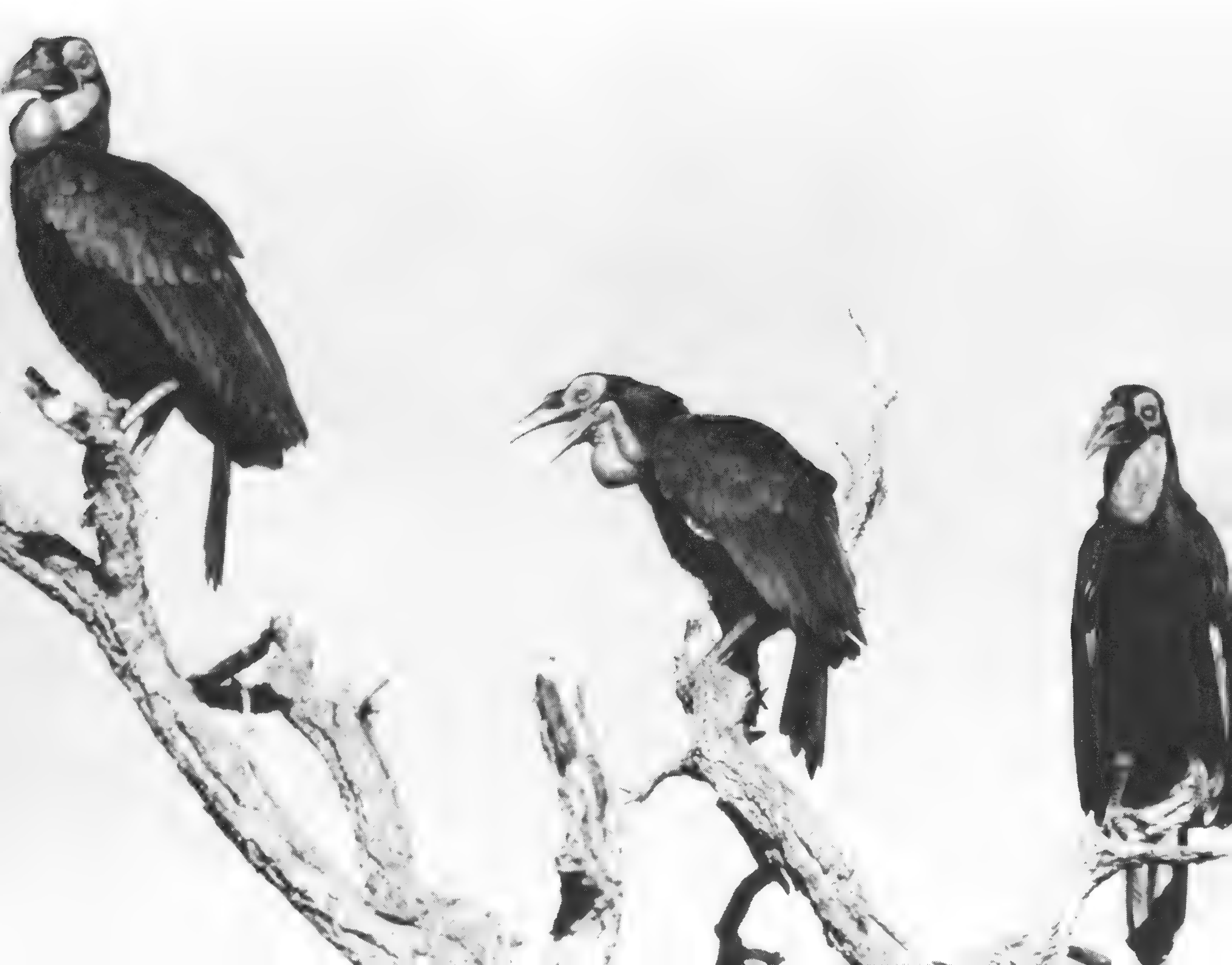


TABLE 2

Distribution of Amblyceran Mallophaga among Hornbill Genera

*Hornbill genera**	*Chapinia species-groups*			*Bucerocolpocephalum*	*Bucerophagus*
	Lophoceros	*Actobulvatum*	*Hirta*		
Ethiopian *Tockus (Tropicranus)*	X				
Oriental *Tockus*		X			
Ptilolaemus				X	
Anorrhinus (Berenicornis)		X		X	
Anthracoceros		X			
Penelopides		X	X		
Rhyticeros (Aceros)		X	X		
Buceros		X			X
Rhinoplax					X
Bucorvus					X
Bycanistes	X				
Ceratogymna	X				

*Genera in brackets have no lice recorded from them.

of *cylindricus* and *subcylindricus*, to the brays of *brevis*. The species breed monogamously but show no evidence of territoriality (Alan C. Kemp, pers. observ.; Kilham 1956; Moreau and Moreau 1941). Indeed they are notorious for feeding and roosting gregariously. All species are mainly frugivorous, even when breeding, but they will take animal food, especially the short-billed *fistulator* (Chapin 1939).

Bycanistes species have been found nesting in holes in forest trees or in rock holes. The nest entrance is sealed by both sexes. Males swallow mud and debris which is formed into pellets and regurgitated to the female. Both sexes, but mainly the female, apply the sealing material (Kilham 1956; Millar 1921; Moreau 1935; Stonor 1937). The female in some species *(fistulator, bucinator)* undergoes a simultaneous flight-feather molt while breeding but in others *(cylindricus, subcylindricus, brevis)* does not (Chapin 1939; Kilham 1956; Moreau 1935; Stonor 1937). The normal clutch of all species appears to be two eggs, but only one young is raised. The younger chick probably dies of starvation (Kilham 1956). The nesting cycle takes about four months, during which the inmates are fed largely on fruit regurgitated by the male. *B. brevis* may bring up to 69 small fruits in one visit. The average of 12 visits daily during the incubation period rises to 21 daily during the chick's development (Moreau 1935). An estimated 24,000 fruits may be delivered to the nest in 1,600 visits over the whole nesting cycle. The chicks develop deep purple body skin, and the female emerges with the chick at the end of the nesting cycle.

Ceratogymna

The two species in this genus are the only large hornbills in the African forests. They are characterized by having bare throat wattles. They have short tarsi and wings and the species differ in the color of the bill and amount of white in the tail. The sexes differ in eye color and females have a brown head and neck instead of black as in males, with plumage of immatures resembling adult females.

Both species have loud braying calls, but they are not as gregarious as *Bycanistes* hornbills and are usually found in family parties. This indicates that they may be territorial, but little of their biology is known. They are monogamous when breeding. Stomach contents of collected specimens indicate that they eat mainly fruit but will take any small animals they encounter (Chapin 1939). They may be the only hornbills that drink water regularly. I have observed a female in the London Zoo drinking, and also a wild specimen in a nature film, but have never seen any other hornbills drinking.

The nest of the Yellow-casqued Hornbill *(C. elata)* is undescribed but that of the Black-casqued Hornbill *(C. atrata)* has been observed in the wild (Chapin 1939; Sanft 1960) and in captivity (Poulsen 1970). Both sexes seal the entrance hole, using pellets formed by the male in the same way as *Bycanistes*. The female does not appear to undergo a simultaneous flight-feather molt while breeding. Two eggs are laid but only one chick appears to survive, to which the male regurgitates food at the nest. Chicks develop deep purple skin, but further details are lacking.

The Mallophaga of Hornbills

The feather lice of birds can be useful indicators of affinities between species, although their value depends on the accuracy of the louse taxonomy and aspects of louse/bird biology which might permit host interchange. This last point may be especially relevant in hornbills where species within one area may regularly interchange nest holes. The lice of hornbills have been well studied (Elbel 1967, 1976). Three genera of amblyceran mallophaga have special bearing on the relationships of the genera of hornbills, and their distribution is shown in Table 2.

Relationships of Hornbill Genera

In understanding relationships within the Bucerotidae, it is necessary to make some comments on related families. Hornbills have long been placed closest to hoopoes (family Upupidae: Upupinae and Phoeniculinae) for a variety of reasons (Sibley and Ahlquist 1972). However, the two families are probably diphyletic, for hoopoes possess a unique form of the stapes (Feduccia 1976) and downy chicks, while hornbills are the only birds with fused axis and atlas vertebrae, a casque on top of the bill, and the sealed-in nesting habit (Kemp 1971; Verheyen 1955). It may be significant that both families have evolved methods of nest defense, hoopoes by smelly secretions and aggressive behavior (Lohrl 1977) and hornbills by sealing the nest entrance (Kemp 1971), suggesting that they were subjected to similar selection pressures. Other suggested relatives of these families with syndactylous feet (order Coraciiformes *sensu lato)* differ in having no nest protection, colors in the plumage other than black, white, or brown, and round shiny eggs versus oval pitted ones. The rollers (Coracii) may be the most closely related to the hoopoes and hornbills, the primitive Leptosomatidae (Cracraft 1971) showing some characters in common with hoopoes such as chick down, egg form, and nest odors (Forbes-Watson 1967). It will be assumed here that hornbills are most closely related to hoopoes but that each family developed independently from similar stock.

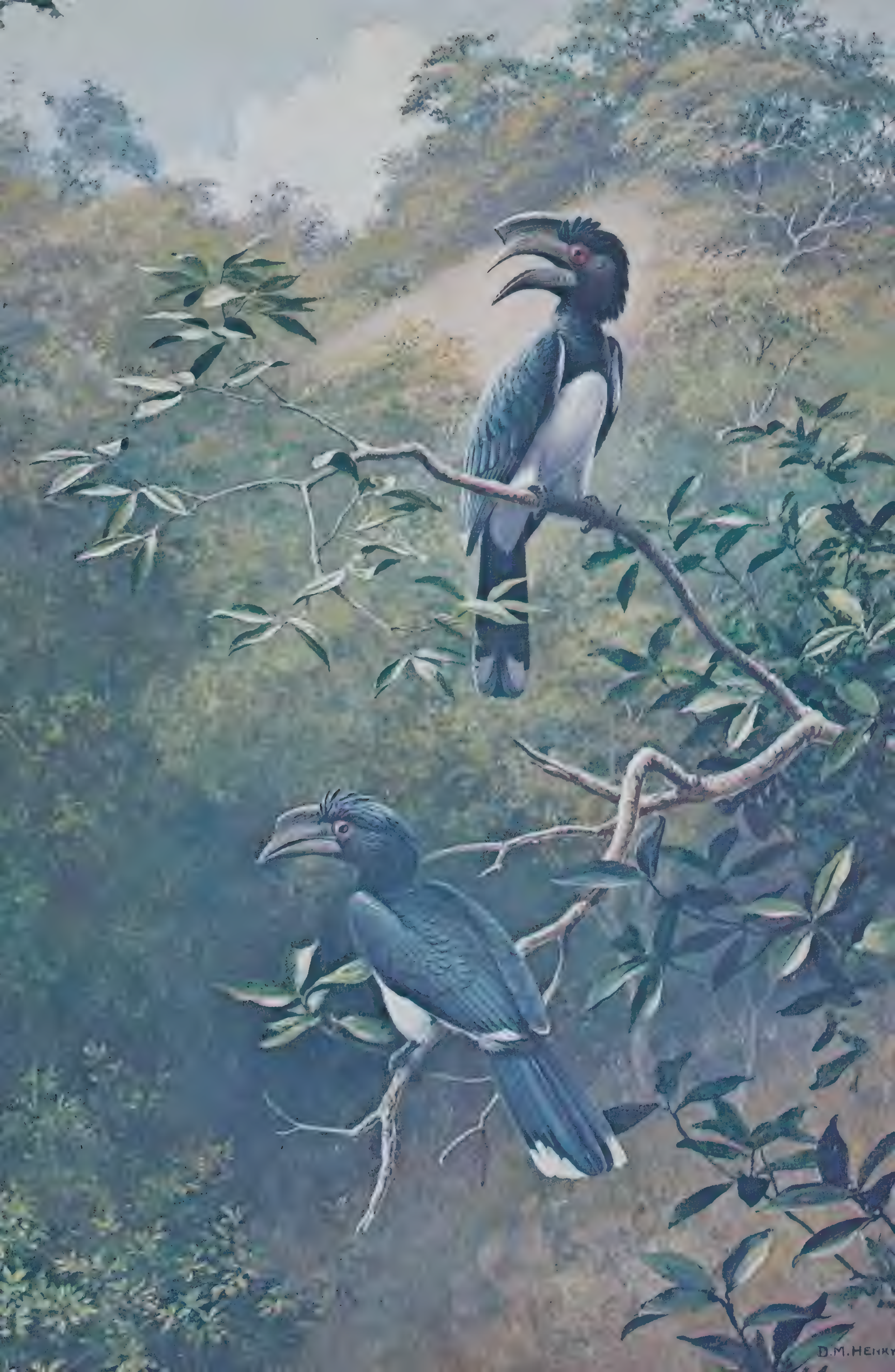
Aspects of the behavior of modern hoopoes may have bearing on understanding the primitive condition in hornbills. Hoopoes utter clucking or hooting calls with the head bowed *(Upupa, Rhinopomastus, Phoeniculus)* and in

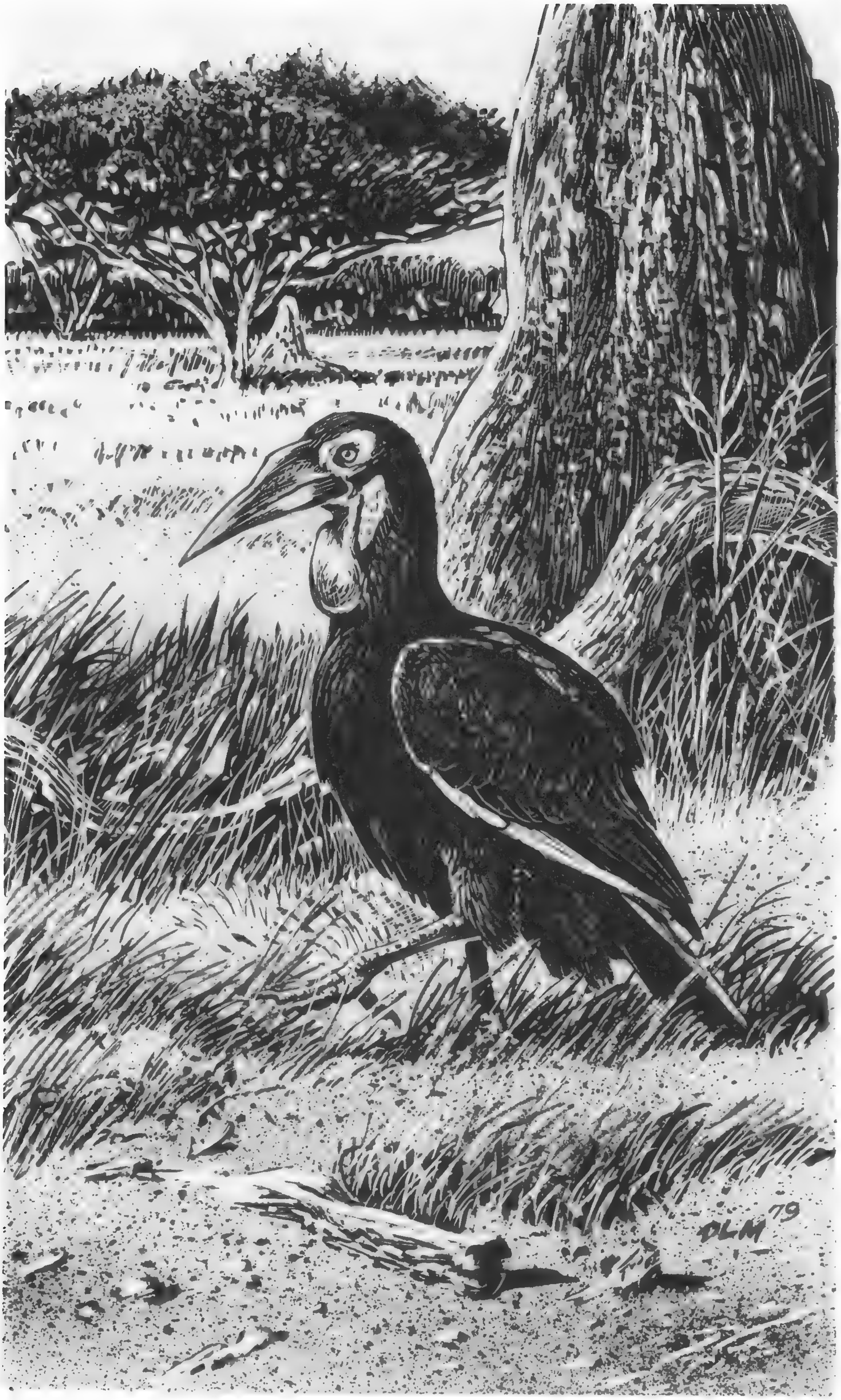
P. purpureus territorial calling is accompanied by rocking back and forth (pers. observ.). In these same genera, the female remains in the nest for the incubation and early nestling periods, being fed single food items by the male, or by the group in the case of *P. purpureus* which is a cooperative breeder (pers. observ.). The chicks have pink skin. Most species of hoopoes have black bills, which is the immature condition in *Phoeniculus* where adults have red bills. In *Scoptelus* and *Rhinopomastus* the sexes may be distinguished by brown head and neck plumage, the immatures resembling either sex depending on the species (Chapin 1939). Several species have white bars in the wing or white tips to the long graduated tail (Phoeniculinae), and most are black in color except for iridescent green and purple structural colors. I suggest that the proto-hornbill was a small species rather like a phoeniculid, with black plumage and bill, and possibly a white wing bar or tail tip. Calling, of a clucking type, probably was uttered with the head bowed. Chicks probably had pink skin. The prolonged feeding of the female during nesting has already been suggested as a preadaptation for developing a sealed nest (Kemp 1971). Once a sealed nest was developed, then the simultaneous molt of flight feathers and nest sanitation could evolve.

It would appear that the Ethiopian *Tockus* species are closest to the hypothetical proto-hornbill, especially the diminutive *hartlaubi* and *camurus*, whose biology unfortunately is little known. The terrestrial foraging Ethiopian *Tockus* species may resemble the primitive condition most closely, giving clucking calls with the head bowed. The whistling calls, given with head turned upward, in the arboreal foraging species are a derived condition. I indicated that *Tropicranus* shows many biological similarities to Ethiopian *Tockus* species and suggest that it be considered a morphologically aberrant member of that genus with primitive coloration (Kemp 1976). I also suggested that the oriental *Tockus* species deserve generic status, for they feed young at the nest by regurgitation, give calls that are probably more convergent than homologous, manifest a lack of complex displays, and have immatures with pale yellowish bills (Kemp 1976). Their separation is also borne out by their lice (Elbel 1967).

Immatures with yellow bills, presumably a primitive condition relative to the adult colors, are shared by several oriental genera—*Tockus, Ptilolaemus, Anorrhinus, Berenicornis, Anthracoceros, Buceros,* and *Rhinoplax*. Several of these genera also have an undeveloped casque, presumably a primitive condition—*Tockus, Ptilolaemus, Anorrhinus, Berenicornis,* and *Penelopides*. On the other hand, *Rhyticeros, Aceros, Penelopides* (except for some populations in the *panini* complex), and *Berenicornis* all have males and immatures with brown or white heads while females have black heads. *Penelopides, Aceros,* and *Rhyticeros* also have ridging of the sides of the bill, on the upper or lower mandible or both. The monotypic genera *Ptilolaemus* and *Anorrhinus*, which appear so superficially similar, are probably closely related as suggested by their sharing a louse genus found on no other hornbills. *Berenicornis* also appears superficially like a large *Anorrhinus*, but so little is known of the species, including its ectoparasites, that its relationships are obscure. *Penelopides* resembles *Anorrhinus* and *Ptilolaemus* in calls, size, and lack of casque development. And some populations of the *Penelopides panini* complex have tails with dark ends and pale bases, a condition shared only with *Anorrhinus* within the hornbills. *Aceros* and *Rhyticeros* appear similar in many ways and almost certainly represent the same evolutionary direction; in fact, they have been considered congeneric (Peters 1945).

Trumpeter Hornbill, *Bycanistes bucinator*. Painting by David M. Reid-Henry. Courtesy of Mrs. D. M. Reid-Henry.


D.M. HENRY



Southern Ground Hornbill, *Bucorvus leadbeateri*. Drawing by Donald Malick.

Anthracoceros may not be a good generic grouping, since the component species represent a diversity of character states. All known species have chicks with pink skin, but in *coronatus* females of one of the two major populations—perhaps distinct species—leave before the chicks, while the females in the other population leave with the chicks. The latter condition also pertains to *malayanus*. Immatures are differentiated from adults by the form of the bill in *coronatus* and *marchei*, as are the sexes; but in *malayanus* the sexes are separable on bill color, with immatures resembling males. In *montani* the sexes are separable on eye color, with immatures remaining undescribed. This uneven distribution of characters is not found in other genera, and cannot be accounted for by different social selection pressures within the species. The oriental *Tockus* species would fit in this heterogeneous genus *(Anthracoceros)* just as well as they do in their current placing. The casque of *T. birostris* resembles casques of *Anthracoceros* more than *T. nasutus*, and it also has elongated central rectrices like *A. malayanus*. The calls of *T. griseus* sound more like those of *A. coronatus* than of any *Tockus* species, although calls are also heterogeneous within *Anthracoceros*.

The genera *Buceros, Rhinoplax*, and *Bucorvus* appear to be closely allied on the basis of their large size, possession of a specialized tuft of feathers on the preen gland, and in sharing *Bucerophagus* lice. *Rhinoplax* is probably best

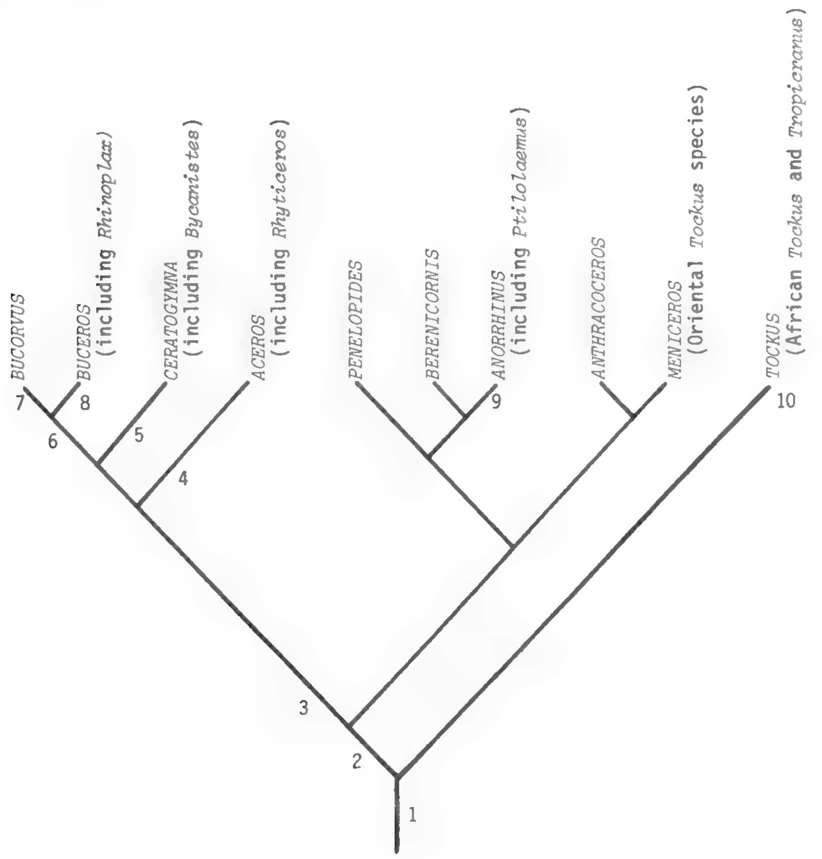

BUCORVUS
BUCEROS (including Rhinoplax)
CERATOGYMNA (including Bycanistes)
ACEROS (including Rhyticeros)
PENELOPIDES
BERENICORNIS
ANORRHINUS (including Ptilolaemus)
ANTHRACOCEROS
MENICEROS (Oriental Tockus species)
TOCKUS (African Tockus and Tropicranus)
7
8
6
5
4
9
10
3
2
1

Figure 12. A suggested phylogeny and generic arrangement of Bucerotidae. The numbers indicate the following suggested derived characters: 1, fused axis and atlas vertebrae, sealed-in nest, casque on bill; 2, regurgitation of food; 3, dark-skinned chicks; 4, males and immatures with brown/white heads and necks; 5, immatures and females alike in bill and plumage, special nest sealing method; 6, large size, special preen gland tufts, presence of *Bucerophagus* lice; 7, colored feet (in contrast to feet that are black or slate gray), specialized anterior casque, cosmetic colors, black tail band; 8, suite of terrestrial and carnivorous adaptations, 15 vertebrae; 9, presence of *Bucerocolpocephalum* lice; 10, complex displays.

considered an aberrant *Buceros*, sharing with that genus colored feet, a black band through the tail, the use of cosmetic coloration, and specialization of the anterior part of the casque. *Rhinoplax* differs from *Buceros* in having greatly elongated central rectrices, nondimorphic eye color, bare head and neck, and a unique hooting call. The only other hornbill with hooting calls is *Berenicornis* which is also one of the larger species. If *Bucorvus* is placed with the *Buceros-Rhinoplax* group, then many of its characters must be seen as secondary reductions, such as the loss or reduction of (1) the casque, the loss of (2) the nest sealing habit, (3) nest sanitation, (4) simultaneous flight-feather molts, (5) habit of regurgitation and its substitution by gathering of a food bolus, (6) the development of booming calls, possibly from the hooting type of call of *Berenicornis,* and (7) bowing of the head during calling. In fact most of the characters so altered in *Bucorvus* can be linked to its adoption of a carnivorous diet and maintenance of an unsealed nest entrance. The carnivorous diet might have been associated with the switch from a forest to a savanna habitat, with the open nest a result of predation and/or over-heating problems in the African savanna.

The genera *Bycanistes* and *Ceratogymna* appear closely allied and more as part of a continuum than as discrete genera. *Bycanistes* species range from small to medium-sized and *Ceratogymna* are large. In the smaller *Bycanistes* species the breeding female undergoes a simultaneous flight-feather molt, but not in the larger species nor in *Ceratogymna*. The immature *Bycanistes* resemble adult females in bill form and have brown foreheads; in the larger *Bycanistes* the cheeks are also brown (as well as specifically colored in adults), while in *Ceratogymna* adult females and immatures have wholly brown head and neck. Both genera have a unique character—*Ceratogymna* with facial skin wattles and *Bycanistes* with a white rump. However, elaboration of the facial skin and reduction of the plumage colors to areas of pure black or white recurs throughout the family. Both genera share the unique method of preparing the sealing material, are largely frugivorous, and have similar lice.

On the information presented here it is possible to offer only a provisional phylogenetic arrangement of the genera (Figure 12).

Evolution of the Hornbills

Any comments on the zoogeographical implications of the suggested relationships, or of any biological trends or convergences within the hornbill family, will only be as good as the understanding of the relationships. The phylogeny suggests that the Bucerotidae are African in origin, as probably are also the Phoeniculinae hoopoes. *Tockus*-like species spread from Africa to the oriental region where they radiated, eventually evolving the large species which recolonized Africa and produced the ground hornbills *Bucorvus* and the forest *Ceratogymna-Bycanistes* complex. This differs markedly from my previous ideas on the family (Kemp 1976) which were based primarily on work with a single genus.

Convergence in several behavioral and biological characters seems to have occurred, indicating that many characters are under ecological control and are genetically flexible. The radiation in calls has been striking, but until a detailed analysis of the calls and of the morphology controlling their production has been undertaken they are of little systematic value. Similarly, reversion to the suggested primitive head-down calling stance appears to have occurred *(Bucorvus)*, and even the head-up stance may have been derived several times. Convergence of displays is strikingly illustrated by the tail-fanning actions of *Tockus hemprichii* and *Aceros nipalensis* which clearly are only distantly related species. The social organization necessary for cooperative breeding has apparently evolved independently in *Anorrhinus galeritus* and *Bucorvus leadbeateri*, and probably also in *Berenicornis comatus, Buceros hydrocorax* and oriental *Tockus* species, based on the social organization and unique immature coloration typical of the cooperative breeders. The ecological correlates of the irregular distribution of such characters as (1) whether immatures resemble the adult male or female, (2) whether a species is territorial or not, (3) whether sex differences (and presumably recognition) are based on eye color, bill shape, bill color, facial skin color, plumage, or a combination of these are not understood at present. Many of these characters vary between obviously related species and will probably be useful in determining interspecies relationships and deciding on species limits.

The suggested loss of the special molt of the breeding female in larger *Bycanistes, Ceratogymna,* and *Bucorvus* may be correlated with high predation pressures in Africa, making it advantageous not to molt when nesting so that escape is easier. *Bucorvus* nests in the savanna, where large cavities may be difficult to seal up or defend. The forest-dwelling *Bycanistes* seem regularly to abandon their nests (Kilham 1956; Moreau 1935). African *Tockus* do not appear to leave their nests often (Kemp 1971), and I have noted that *Bycanistes bucinator* (one of the species that does molt) breeds and roosts away from the habitat in which it normally spends the day and feeds. The transport of food to the nest seems to have initially been solved by the development of regurgitation and subsequently in *Bucorvus*, by forming a food bolus. Notably, *Tockus monteiri* may show convergent behavior to *Bucorvus* in carrying several food items to the nest at once (Kemp and Kemp 1972).

The casques of hornbills, which so characterize the group, appear to have been elaborated for several reasons and on several occasions. In *Anthracoceros* there is little sexual dimorphism and no apparent feeding function of the casque so that it may serve for specific recognition. In *Bycanistes* and *Ceratogymna* the casque is strikingly dimorphic sexually, as it is in *Anthracoceros malayanus*, suggesting sex recognition as a function. In *Buceros* and *Rhinoplax* the anterior part of the casque is specialized and shows little sexual dimorphism, indicating a function in adults which may be for feeding and fighting. Finally, in *Rhyticeros* the casque is variously wrinkled or wreathed and similarly developed in both sexes and appears to function as a species recognition signal. Remember that in many hornbills (18 species) the casque is only slightly developed.

The reasons for the timing of the female's emergence from the nest—probably linked with energy balances in provisioning the nest—and of the development of dark skin in chicks remain to be elaborated.

It is my intent in this study to show the value of relatively simple characters in understanding the relationship of hornbills. Such a systematic study not only permits predictions for species that are little known but have obvious relatives, but also allows predictions of biological information once character suites are identified, such as those associated with cooperative breeding. The characters used here are only those for which sufficient comparative information is available. In a study of a single genus (Kemp 1976) I found that several other characters such as nest lining material, presence or absence of particular calls, roost sites, and sunbathing postures may also be predicted. Many of these characters are observable in captive birds. And now that several hornbills have been bred in captivity, the basic biology of rare or inaccessible species might become known. Any information from zoos, personal observations, tape recordings, or obscure literature will help in detailed systematic study of the hornbills which I am continuing.

Acknowledgments

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BREEDING ECOLOGY OF THE CLAY-COLORED SPARROW

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The Clay-colored Sparrow *(Spizella pallida)* is a common and widespread breeding bird of dry uncultivated brush regions of the great plains (Root, *in* Bent 1968), and Breeding Bird Surveys (Erskine 1978) indicate that it is probably the most numerous breeding passerine of low shrub communities of the southern parts of the Canadian prairie provinces. Its nesting biology has been looked at in Michigan (Walkinshaw 1939, 1944), in Saskatchewan (Fox 1961), and in Alberta (Salt 1966), but much of this work has been based on casual observations and is anecdotal. Many basic aspects of the breeding ecology of the Clay-colored Sparrow remain essentially undescribed, such as the occurrence and degree of site tenacity, factors which influence nesting success and nest site selection. Finally, there appears to be some confusion concerning the response of Clay-colored Sparrows to brood parasitism by the Brown-headed Cowbird *(Molothrus ater)*, ranging from intolerance (Salt 1966) to acceptance (Root, *in* Bent 1968, Fox 1961) of the parasite's egg. This paper attempts to fill these gaps.

Methods

Study Areas

I carried out this study (Knapton 1978b) in Edward Municipality in extreme southwestern Manitoba, near the towns of Lyleton and Pierson. The topography of this region is gently rolling, at an average elevation of 490 meters above sea level. Originally, the area was mixed-grass prairie (Weir 1960), but modification of the vegetation through human settlement and containment of prairie fires has resulted in the proliferation of aspen *(Populus tremuloides)* bluffs and extensive stands of low shrubs, particularly snowberrry *(Symphoricarpos occidentalis)* and American silverberry *(Elaeagnus commutata)*. It is in these low shrub communities that Clay-colored Sparrows reach their highest densities.

I chose two study plots, both incorporating large expanses of shrub communities along with aspen bluffs and areas of grass (Figures 1 and 2). Study Area 1 was a 5.86-hectare plot located about two kilometers west of Lyleton. It included part of an unused and overgrown road right-of-way and part of a large pasture which was lightly grazed in the first summer and the first half of the second summer of the study. On 14 August 1975, about 4,200 square meters of shrubbery were cut down on the southern boundary of the area, thereby reducing the amount of nesting habitat available to the sparrows in 1976 by about 15 percent. Study Area 2 was 5.67 ha in size, and was located on the Pierson Wildlife Management Area, some seven km southwest of Pierson and about 12 km northwest of Study Area 1. The areas covered by various types of vegetation on each study area were determined by compensating polar planimeter from aerial photographs.

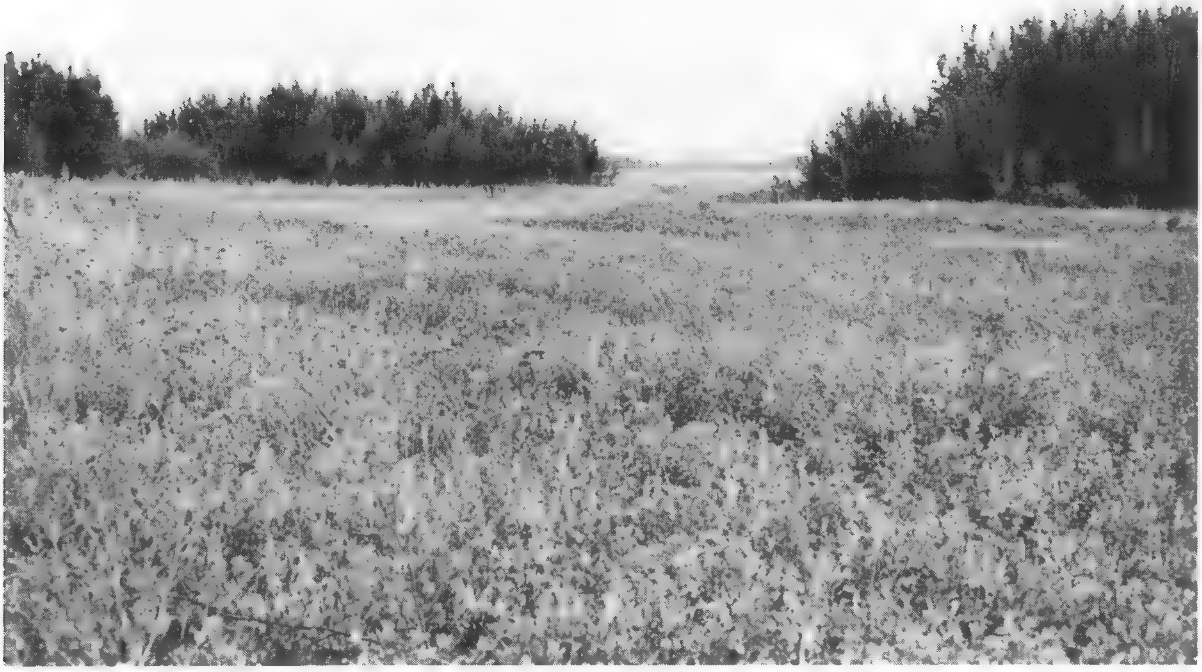


Figure 1. One of the study areas, showing the topography and habitat in which the Clay-colored Sparrow bred.

I spent the following periods on the study areas: 15 May to 15 September 1974; 27 April to 3 September 1975; 30 April to 31 August 1976. These dates coincide with the approximate arrival and departure dates of the Clay-colored Sparrows in southwestern Manitoba. Daily observations were made during the height of each breeding season, each study area being visited on alternate days. A final visit to the areas was also made on 28 and 29 May 1977.

Capturing and Sexing Techniques

I captured adult and immature Clay-colored Sparrows in mist nets, and banded nestlings at about five days of age. Each bird received an aluminum band plus two colored plastic bands in different permutations for individual recognition. In total, 834 birds were banded.

Male and female Clay-colored Sparrows are morphologically quite similar. Hand-held birds in reproductive condition could usually be sexed by the presence of a cloacal protuberance in the male and a brood patch in the female. Both in the field and in museum skins of birds of known sex, males had, on the average, longer wings and whiter superciliary stripes than females (Knapton 1978a). These criteria were supplemented in the field by behavioral differences between the sexes (Knapton 1978a).

Nesting Data

Nests proved to be fairly easy to locate. I located 232 nests: 41 in 1974, 84 in 1975, and 107 in 1976. I visited each nest every other day, and compiled a log of the status of each nest.

During the study, I measured (1) the substrate of the nest, including the proportion and identity of the supporting vegetation, (2) the height from the base of the nest to the ground, and (3) the distance from the surface of the vegetation to the nest rim. I determined the surface of the vegetation as that level at which a ruler held vertically from the nest rim was about 90 percent obscured by the vegetation.

In 1976, I further measured each nest for the degree of concealment afforded it by the nesting substrate by taking a light-meter reading of the amount of penetration of incident light.

I determined the start of the nest initiation from my own data and from that of Fox (1961), Salt (1966), and Walkinshaw (1944). I allowed four days between the start of nest construction and the onset of egg laying, determining this value from the following information: I found six nests in the first stages of construction, each of which contained one or two eggs on the fifth day after its discovery. Also, Fox (1961) found that nest construction required two to four days in four pairs he observed. I allowed four days for the laying of a four-egg clutch. The incubation period has been determined as 10 days (Salt 1966) or 11 days (Fox 1961; Walkinshaw 1944). I found the incubation period between the laying of the last egg and the hatching of the last egg to be about 11 days for 13 nests (range approximately 10 to 12 days). Thus, a total of 19 days elapsed between the initiation of the nest and the hatching of the last young.

Cowbird Parasitism

I treated cowbird parasitism in the following manner. When I had located a nest containing a cowbird egg, I left the egg in the nest for a minimum of four days in order to determine the response of the host to the parasite's egg. On Study Area 1 in 1974, I left the eggs in the nest and followed the progress of the nest. In all other cases, I removed the egg on or after the fourth day.

Light Penetration Analysis of the Shrubbery

As there appeared to be a consistent tendency to use a snowberry bush over other available shrubs as a nest site in 1974 and 1975, in 1976 I objectively measured light penetration within the shrub communities. Aerial photographs of each study area were divided into 10m² sections, and the rows and columns numbered. A section of shrubbery was determined by random sampling of a pair of numbers, one from the rows and the other from the columns. This selection process was continued until there were ten samples of wolfberry and ten of other shrubs, usually American silverberry, for each study area. Then a three-meter stick was tossed into each of the chosen sections of shrubbery, the stick held upright, and penetration of incident light, using a light meter, was recorded at ten-centimeter intervals to the top of the vegetation.

Territoriality

Arrival on the Breeding Grounds

Clay-colored Sparrows arrived on their breeding grounds in southern Manitoba in early May (Figure 3). Males arrived before females in both

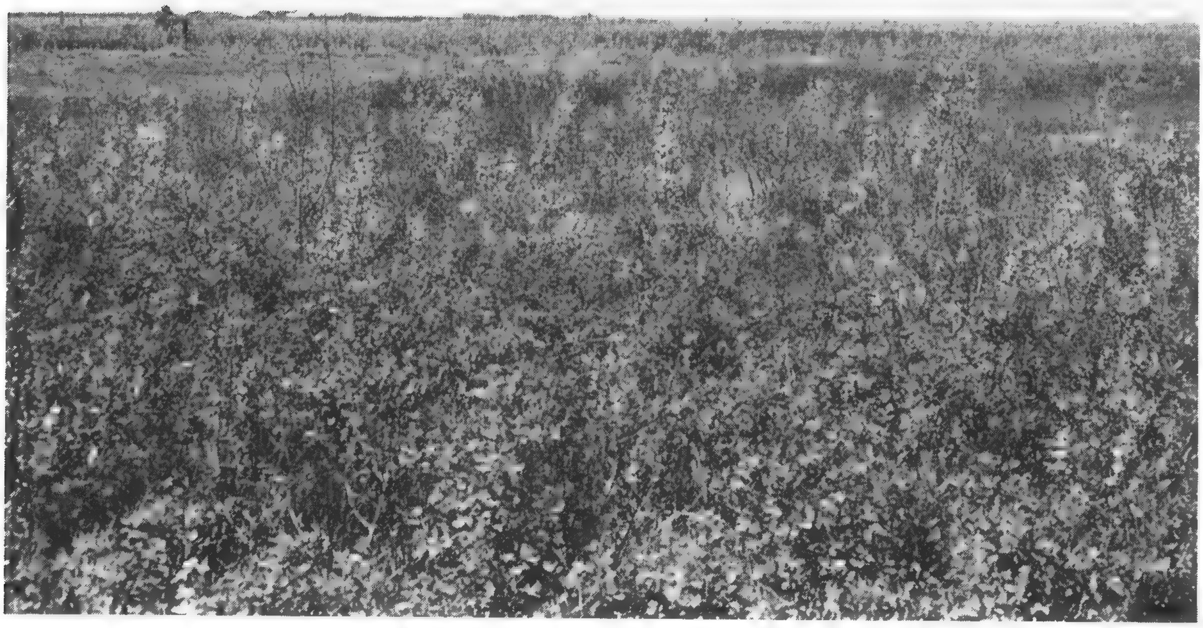


Figure 2. One of the study areas, showing the topography and habitat in which the Clay-colored Sparrow bred.

years, the major influx occurring from 7 to 10 May (males) and 12 to 16 May (females).

Males and females arrived slightly earlier in 1976 than in 1975 (Figure 3). This may have been due to the mean temperature in April which was 6°C higher in 1976 than in 1975. This might have accelerated the northward migration of the flocks of Clay-colored Sparrows in 1976 if the warmer temperatures extended south, as well.

Site Tenacity and Territorial Exchanges

Analysis of returns to the study areas revealed that males showed a high rate of return to the vicinity where they had nested the previous year (Table 1). On Study Area 2, the number of returning banded males was consistently high, between 62 and 85 percent. The return of males on Study Area 1 ranged between 46 and 59 percent, and this range was significantly lower than that on Study Area 2 ($X^2 = 5.14$, $P<0.05$; two by two contingency table for all years combined). The return rates of male Clay-colored Sparrows on Study Area 2 compare favorably with those of other grassland or shrub

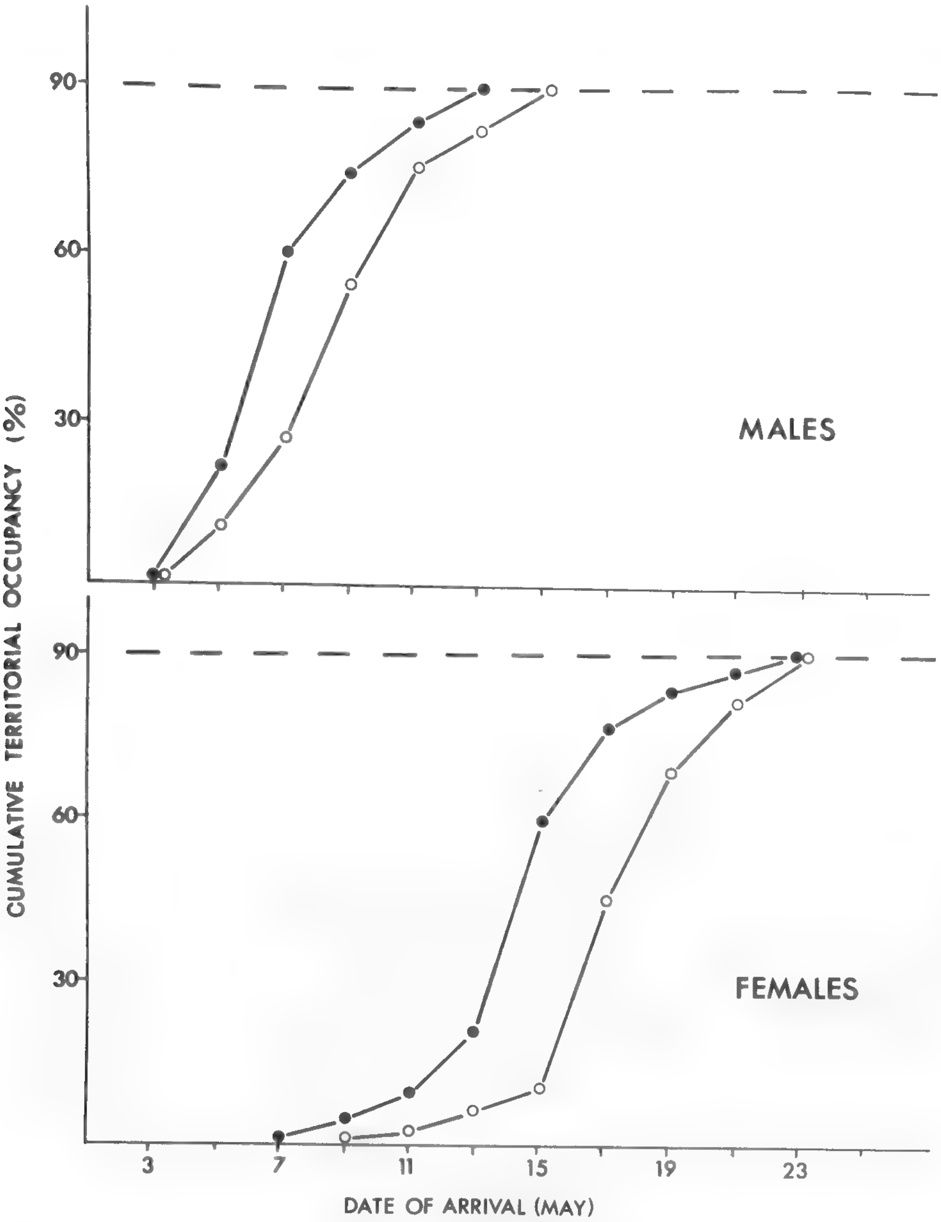


Figure 3. Dates of arrival of male and female Clay-colored Sparrows, both study areas combined. N=66 territories in 1975 (open circles), 67 territories in 1976 (solid circles).

TABLE 1

Return Rates of Male and Female Clay-colored Sparrows to the Study Areas

	Year	*Number of territorial pairs*	*Number and percentage of birds returning the following year*	
			Males	*Females*
Study Area I	1974	17*	9 (52.9)	5 (29.4)
	1975	27	16 (59.3)	4 (14.8)
	1976	22†	10 (45.6)	3 (13.6)
Study Area 2	1974	36*	24 (66.7)	5 (13.8)
	1975	39	33 (84.6)	8 (20.5)
	1976	45	28 (62.2)	7 (15.6)

*Not all territorial pairs present on the study areas were banded in this year.

†The decline in numbers of territories from 1975 to 1976 was partially due to the loss of shrubbery, which eliminated four territories.

inhabiting species; the return rates of males on Study Area 1 rather less so (Table 2).

Not only do the males return to the same general area but most often (76% in 1976) to the same territory; and they often reoccupy the same song perches. Occasionally adjacent males exchanged territories in successive years. Usually only two territorial males were involved in such a shuffle. Five territorial exchanges (three on Study Area 1, two on Study Area 2) occurred between 1975 and 1976, and of the ten males involved seven had not raised any young in 1975. This raises the possibility that territorial exchanges and nesting success may be correlated. However, on Study Area 2, three males holding adjacent territories in 1975 exchanged them with each other in 1976; all three males had bred successfully in 1975. Thus, not all shuffling of territories between years was a result of nesting failure, although the reasons behind this triple shuffle remain obscure. In 1976, two of these three males fledged young.

Return rates of female Clay-colored Sparrows on both study areas were significantly lower than those of males ($X^2 = 84.2$, $P<0.001$ for all years combined), being about 14 to 29 percent (Table 1). High female mortality during the non-breeding season was ruled out, since one female was known to be at least four years old at the end of the study, and nine others were known to have reached at least the age of three years. The return rates of females were also appreciably smaller than those of females of most species in Table 2. In general, a female did not return to the same territory as the year before, even if she had fledged young there the previous year. Hence, of 32 females that returned to the general area, 29 (90.6%) did not mate with the previous year's male.

There was one exception to this trend; one pair occupied the same territory and stayed together for three consecutive summers on Study Area 2, an event most unlikely to have occurred by chance. The fact that flocks of Clay-colored Sparrows on the wintering grounds in Mexico appear to be composed of both males and females (Knapton 1978) suggests that males and

TABLE 2

Return Rates to Breeding Areas of Some Open Country Species of Passerines

Species	*Average return rates (percentage)*		*Reference*
	Male	*Female*	
Skylark *(Alauda arvensis)*	70	62	Delius 1965
Bobolink *(Dolichonyx oryzivorus)*	62.8	39.9	Martin 1974
Seaside Sparrow *(Ammospiza maritima)*	55	28	Post 1974
Song Sparrow *(Melospiza melodia)*	62	42	Nice 1937
Field Sparrow *(Spizella pusilla)*	44	12	Best 1977a
Clay-colored Sparrow *(S. pallida)*			
Study Area 1	52.6	19.3	This study
Study Area 2	71.2	16.6	

females could conceivably stay together all year. This seems somewhat unlikely under normal circumstances, however, since males arrive on their breeding grounds several days before the females, indicating a temporal separation of the sexes at least during spring migration.

During the course of the three summers, 146 nestlings and 305 immatures were banded. No individual banded as a nestling and only four banded immatures (2 of each sex) were recorded in subsequent years on the study areas. This is in contrast to a return rate in Song Sparrows *(Melospiza melodia)* of 12.6 percent (Nice 1937) and in Skylarks *(Alauda arvensis)* of 8.8 percent (Delius 1965).

Establishing Territories

Male Clay-colored Sparrows started to establish territories on the day they were first observed on the study area. Establishment and subsequent defense of the territory involved singing, especially from perches near the territorial boundaries, and overt aggression between individuals. Once boundaries between contiguous territories were established, neighboring males trespassed only rarely, and aggressive interactions between individuals declined considerably by mid-May.

In 1976, I quantified this trend by measuring hostile encounters throughout the breeding season. I observed 71 aggressive interactions between individual Clay-colored Sparrows in 1976, 26 on Study Area 1 and 45 on Study Area 2. Of these, 64 were chases and 7 were fights. In every case, the protagonists, when identifiable, proved to be males; in no instance was a banded female observed in a hostile encounter. Most encounters involved neighboring territorial males, which were readily identifiable by their colored leg bands. Six encounters involved unbanded birds, and, for the purpose of analysis, an unbanded bird was assumed to be a new male, a reasonable assumption considering that all territorial males in 1975 had been banded and that the conflict area was part of a vacant territory subsequently occupied by a new male. The outcome of most encounters was easily determined; in four instances, however, roles were reversed when territorial boundaries were crossed and the chaser became the chased.

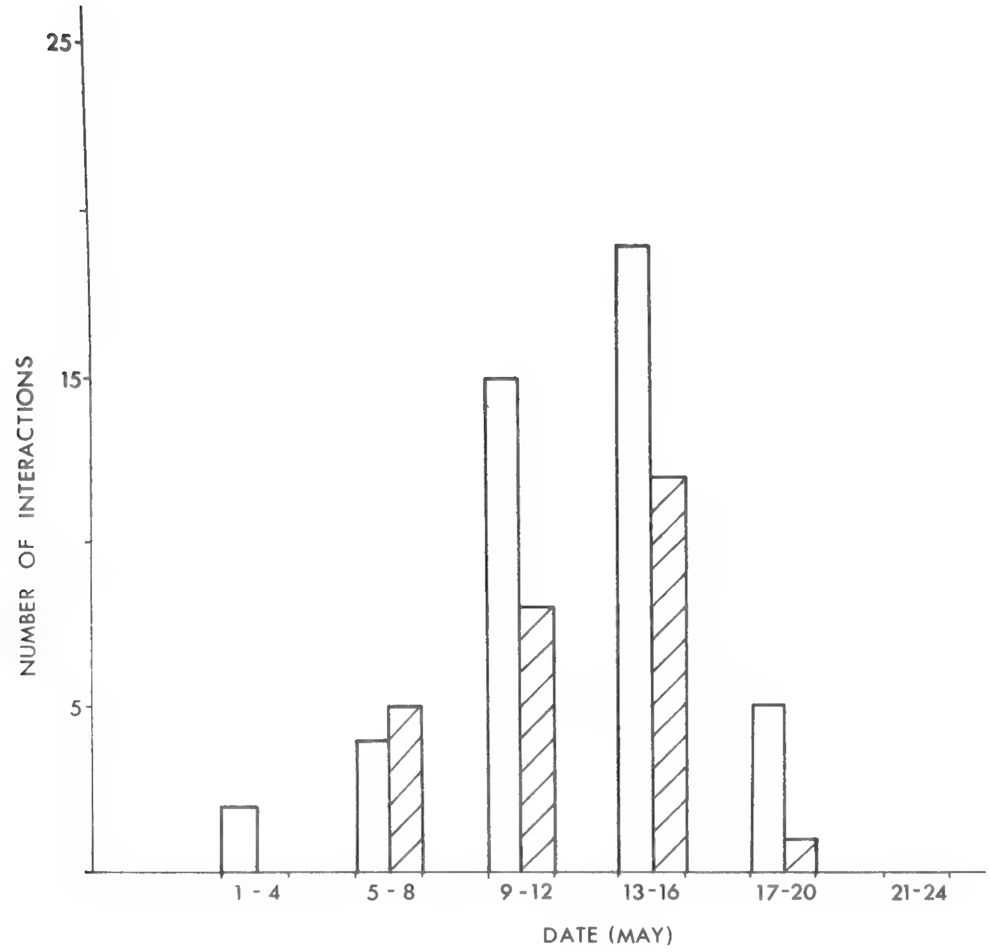


Figure 4. Total number of aggressive interactions among male Clay-colored Sparrows during the breeding season. Study Area 1, hatched bars; Study Area 2, open bars.

Over 95 percent of interactions on Study Area 1 occurred from 4 to 16 May, and over 85 percent of interactions on Study Area 2 between 8 and 16 May (Figure 4). No overt aggressive interactions were observed on either study area after May 20. This suggests that most interactions involved the establishment of territorial boundaries. Returning males participated in relatively few aggressive encounters among themselves, but encounters between returning males and new males, and among new males themselves, were markedly more frequent. There were proportionately more returning males (33) than new males (12) on Study Area 2, yet only 13 percent of all interactions were between returning males. Similarly, on Study Area 1 returning males, although outnumbering new males 13 to 9, produced only 8 percent of all interactions among themselves.

The Mating System

The pair bond in the Clay-colored Sparrow during the breeding season on my study areas was stable. Once paired, the members of a pair stayed together throughout the breeding season, even if they incurred successive nest losses. Monogamy prevailed on my study areas; no example of any other type of mating system was recorded.

The Nesting Season

The nesting season of the Clay-colored Sparrow in southwestern Manitoba extended from May to early August. The length of the breeding season may have been long enough for individual pairs to raise more than one brood per season. In 1975, however, pairs that successfully raised young did not attempt a second brood, even though young were out of one nest by 12 June. In 1976, the situation was almost the opposite. Of 20 pairs that fledged young prior to 23 June, 11 (55%) attempted to raise second broods; five pairs were successful. No pair that fledged young after that date attempted to raise another brood.

An analysis of the start of construction of nests that ultimately contained eggs showed that the 1976 breeding season started earlier than in 1975. Of 30 nests initiated in May 1975, only one was started before 23 May, whereas in May 1976, 14 nests out of 44 were started before 23 May.

Furthermore, in 1975, new pairs took over some territories and attempted to breed midway through the breeding season, in late June and early July, after territories had been vacated by successful pairs. Seven such changeovers took place. Of the 14 males involved, none of the original seven males returned the next year, whereas three of the replacement males returned. No female from either an original or a replacement pair was resighted; this is perhaps not unexpected as site tenacity and mate fidelity in females were low.

The Nest

Vegetation Analysis of the Substrate

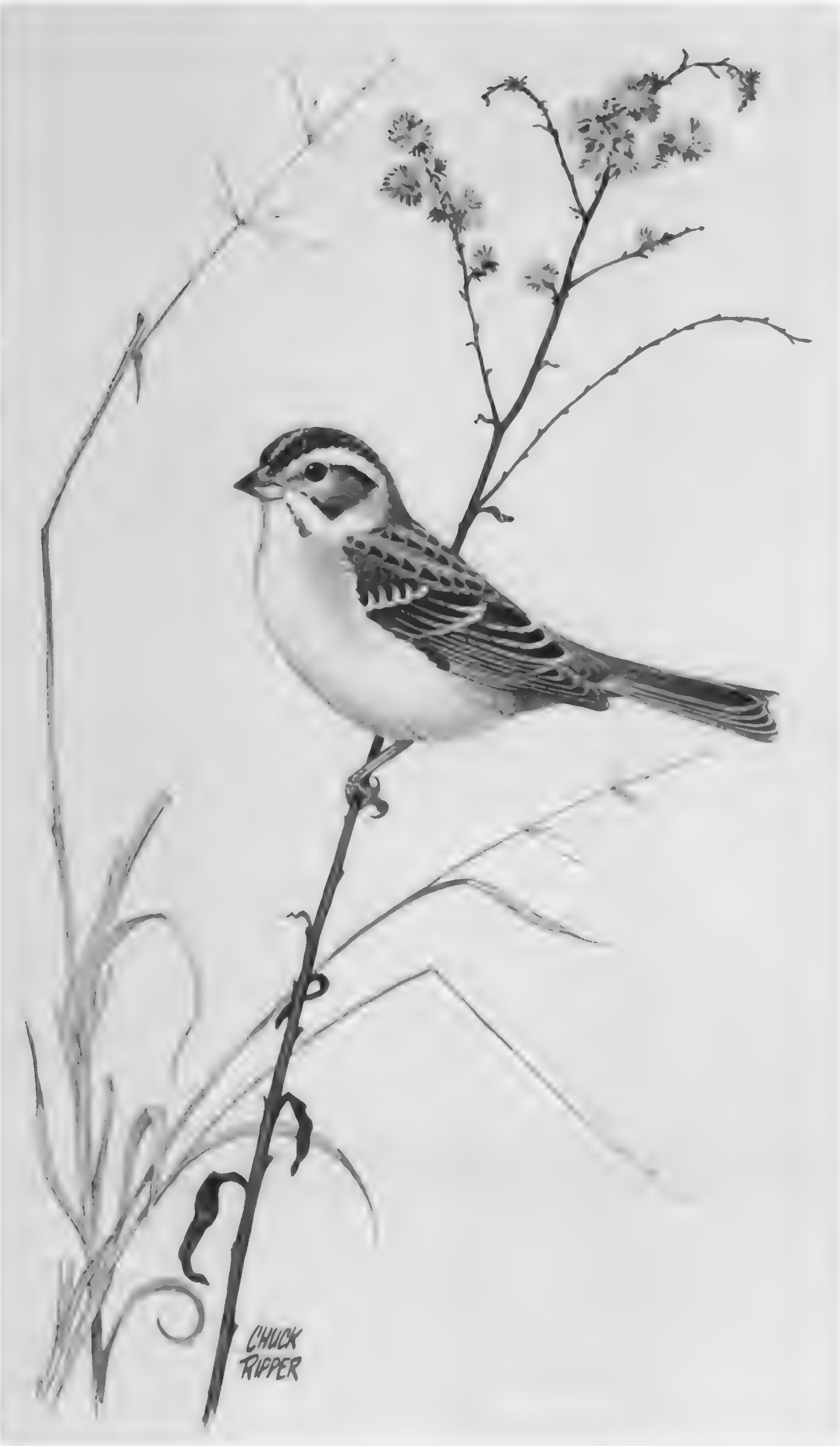
Tendencies within a local population of Clay-colored Sparrows to use one type of nesting site above all others have been reported by Fox (1961), Salt (1966), and Walkinshaw (1939). Such a tendency was also evident in both populations I studied in southwestern Manitoba. Out of 125 nests, 110 were built wholly or mainly in snowberry (Figure 5). Only six nests contained no snowberry in the support of the nest.

In 1976, I counted the number of branches and/or stems supporting 107 nests. Numbers of supports ranged from 4 to 18. Of the three main vegetation types present (Table 3), there is once again an overwhelming use of snowberry as the nest substrate; 87 nests (81%) were mainly or wholly supported by snowberry, and only five (5%) nests did not contain at least one branch of snowberry in the nest substrate.

In order to show that Clay-colored Sparrows prefer snowberry as a nest substrate over potentially available sites in other vegetation, it is necessary to compare the frequency with which a particular type of vegetation is used in proportion to its availability in the habitat. There was a pronounced preference for snowberry as a nest substrate. Significantly more nests were built primarily in snowberry than would have been predicted by chance ($X^2 = 15.4$, $P<0.001$). Snowberry accounted for 58.0 percent by area of the shrubbery and grassy regions of the study areas, yet 83.7 percent of the 104 nests used in the analysis were constructed in snowberry. Snowberry accounted for 89.0 percent of the vegetation within the territories of the sparrows.

Grass stems were incorporated into the nest substrate slightly more than expected (Figure 6), possibly a result of the tendency of pairs to construct their nests at the edge of a patch of snowberry (Knapton 1978b), where there may have been proportionately more grass present than in the center of a patch.

I next compared light-meter measurements between snowberry and other types of shrubbery, primarily American silverberry, and found that


CHUCK
RIPPER

Clay-colored Sparrow, *Spizella pallida.* Drawing by Chuck Ripper.

significantly less light penetration occurred in snowberry at all levels above the ground than in the other vegetation.

Nest Location

Salt (1966) and Walkinshaw (1944) reported that early nests are closer to the ground than later ones. Salt (1966) further suggests that the Clay-colored Sparrow is more responsive to distance of the nest from the surface of the surrounding foliage than from the ground, so that nest height increased as the season progressed and the vegetation grew taller and denser.

No such seasonal trend in nest height was obvious in this study. Height range above ground of the nests at any one time was broad and was not correlated significantly with time of season. In general, however, nests were constructed close to the ground throughout the breeding season, only 15 percent being higher than 30 cm above ground in 1976. Similarly, there was no significant tendency to construct a nest at a set distance below the top surface of the vegetation, the 1974 data producing a random scattering of values throughout the nesting season for both study areas combined, $r = 0.17$. Rather, pairs tended to construct their nests at certain heights above ground regardless of the season, individual pairs tending to be consistently ground, low, or high nesters within a season for both study areas combined, $r = 0.76$, $P<0.01$.

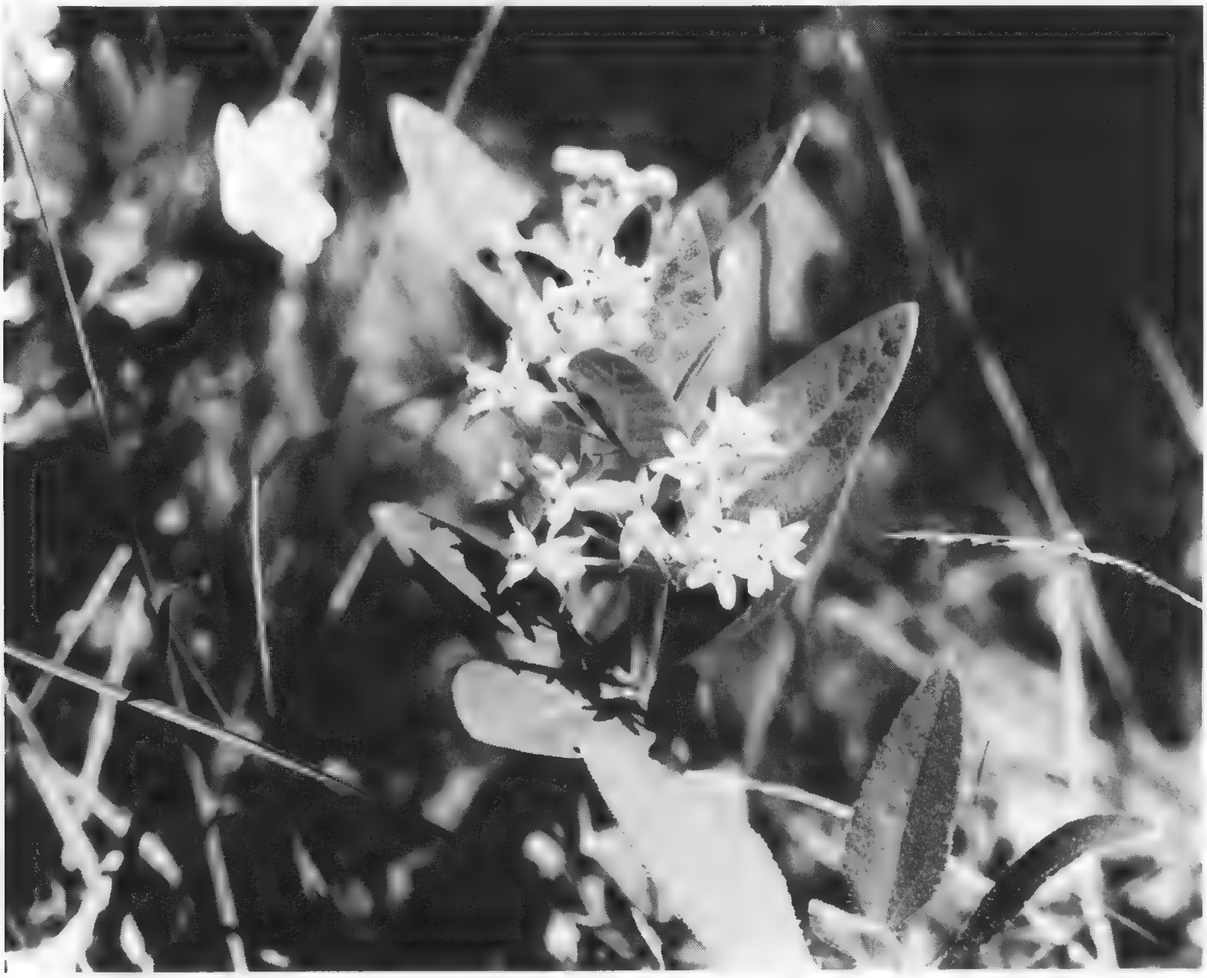


Figure 5. Clay-colored Sparrows showed a strong preference to build their nests in snowberry, *Symphoricarpos occidentalis*. This shrub served as a partial or complete support for 119 of 125 nests in southwestern Manitoba.

TABLE 3

Comparison of Number of Nests of Clay-colored Sparrows and the Proportion of Three Types of Vegetation Used as Nest Substrate

Percentage of vegetation type as substrate	*Numbers of nests in each vegetation type**		
	Snowberry (Symphoricarpos)	*American silverberry/rose (Elaeagnus/Rosa)*	*Grass/forbs*
0	3	82	22
1–25	5	13	40
26–50	12	9	31
51–75	45	2	9
76–99	27	1	2
100	15	0	3
Total nests	107	107	107

*Each nest is represented three times, once in each vegetation type, according to the amount (percentage) of each vegetation type supporting the nest. Out of 107 nests, 104 contained more than 50 percent of one type of vegetation.

There was no consistency of nest height between years in a particular male's territory. This suggests that females select the nest site since they did not usually nest in the same territory in consecutive years.

Mortality

Adult Survival

Once territories had been established and the territorial pairs identified, then adult losses could be monitored over the season. Adult survival during the breeding season was high. No disappearance of adults during the breeding season could be attributed unequivocally to predation. The only evidence of possible predation on adults occurred at a nest destroyed on 18 July 1976. Two adult rectrices were found near the nest. The female of that nest was not resighted.

Ten males and one female were at least four years old at the end of this study, since we banded them as adults in the spring of 1974 and they held territories in 1977. Root (*in* Bent 1968) reported that a banded Clay-colored Sparrow reached an age of five years.

Nesting Mortality

Table 4 shows the causes of mortality. In this analysis, parasitism by Brown-headed Cowbirds included only those instances in which a Clay-colored Sparrow nest sustained a known loss (eggs or young) and contained a cowbird egg. Predation accounted for the greatest losses of eggs and young, although cowbird parasitism contributed substantially to egg loss. For the two areas combined, predation accounted for 59.5 percent of the eggs lost and 95.3 percent of the young destroyed. Cowbird parasitism accounted for the loss of 2.16 percent of the eggs laid. Most losses (44.9% for the study areas combined) occurred in the egg stage, the proportions being similar between the two areas.

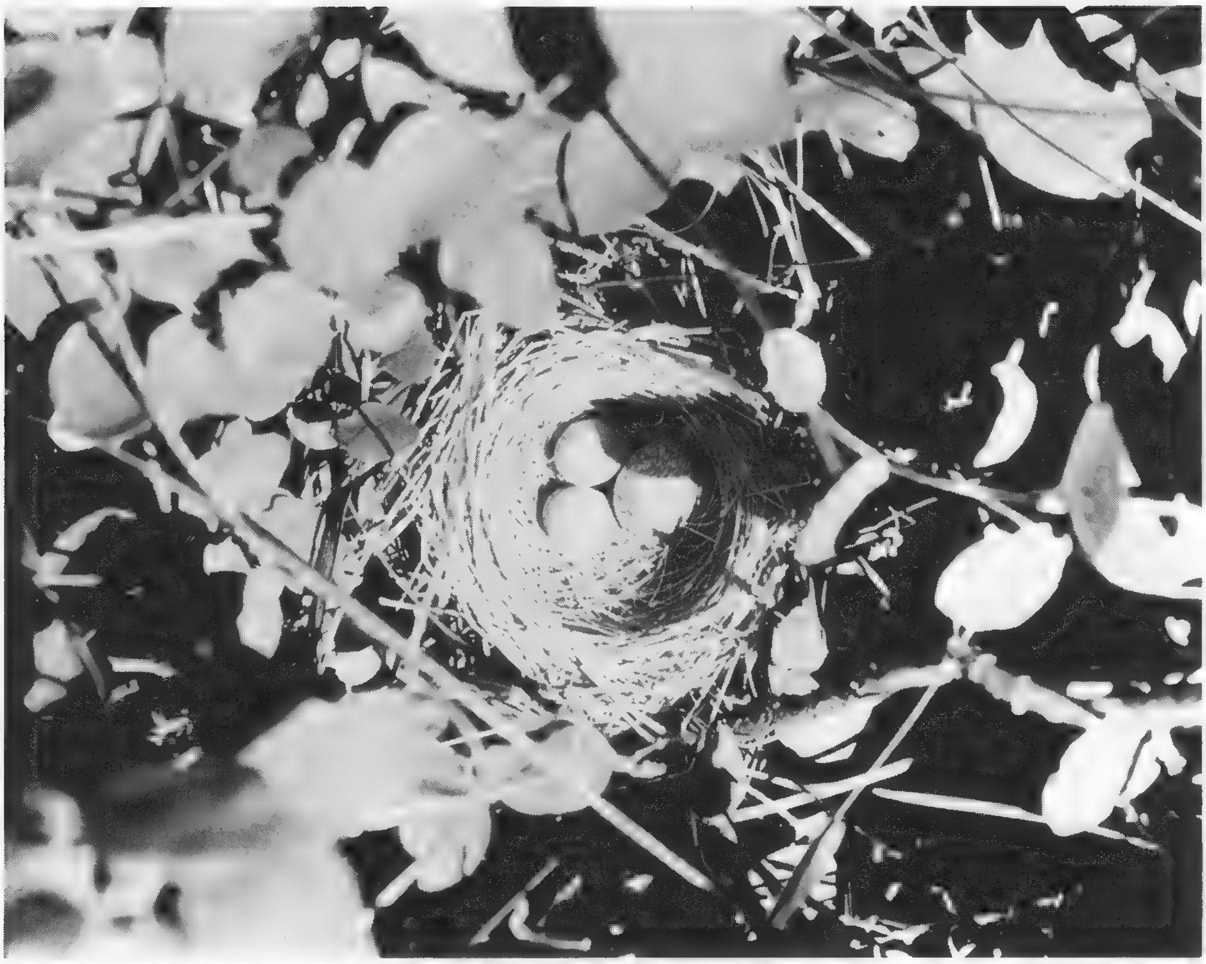


Figure 6. The nest of Clay-colored Sparrows, showing the heavy use of grass stems in the nest substrate. A high percentage of nests contained cowbird eggs. This nest parasitism accounted for significant loss of eggs.

Predation

Potential predators on nests of the Clay-colored Sparrow are numerous and varied (Root, *in* Bent 1968). Further potential mammalian predators not listed in Bent (1968) on both study areas in southwestern Manitoba include the Franklin Ground Squirrel, *Spermophilus (=Citellus) franklini* (Banfield 1974; Sowls 1948) and the Thirteen-lined Ground Squirrel, *C. tridecemlineatus* (Robins 1971, but see Banfield 1974).

An analysis of the predators' behavior showed that predators destroyed the entire contents of 41 out of 52 nests during a single visit. Most of these nests tended to be tipped or damaged, suggesting that ground hunting mammals were the chief predators. The successive removal of eggs from a nest over a number of days is more difficult to explain. Small rodents might have been involved in such predation (Bent 1968:762, 1231), as might cowbirds. In the only predation witnessed, a garter snake *(Thamnophis sirtalis)* swallowed a young Clay-colored Sparrow.

Nesting Success

In the following analyses, a successful nest is defined as one in which one or more Clay-colored Sparrows fledged. Two nests on Study Area 2 in 1976 were omitted from the analyses, because the fate of the young was unknown.

Nest Height

Nests with bases constructed within 10 cm of the ground were significantly more successful than those constructed higher in the vegetation (Figure 7); Study Area 1: $P = 0.0396$, Fisher's Exact Probability Test; Study Area 2: $X^2 = 7.94$, $P<0.025$). For both study areas combined, 28 (61%) out of 46 nests constructed within 10 cm of the ground were successful, whereas only 18 (31%) out of 59 constructed above 10 cm were successful.

Nest Concealment

As noted earlier, Clay-colored Sparrows on both study areas most often constructed their nests in snowberry. However, some nests were obviously less well concealed than others, and I hypothesized that more open nests were subjected to greater predation pressure than those that were better concealed. I therefore compared light-meter measurements between successful and unsuccessful nests in 1976. The combined sample size was 105 nests.

Light penetration at successful nests was significantly lower than that at unsuccessful nests on Study Area 1 ($t = 2.42$, $P<0.05$) and on Study Area 2 ($t = 2.08$, $P<0.05$). This suggests that nests built in vegetation that allowed greater light transmission were more easily detected by predators.

Returning Males

Since male Clay-colored Sparrows showed a high degree of site tenacity, I was able to compare nesting success of returning males and of new males establishing a territory for the first time. Of 20 returning males in Study Area 1, 13 were successful, whereas only 2 out of 10 new males bred successfully there. In Study Area 2, the figures are 24 out of 29 returning males successfully breeding and only 7 of 13 new males. These results indicate that returning males on Study Area 1 enjoyed a significantly higher degree of nesting success than new males ($X^2 = 5.23$, $P<0.025$). On Study Area 2, nesting success was also somewhat higher for returning males (45%) than for first year males (35%), but the difference was not significant ($X^2 = 0.46$). Thus, in general, older birds probably have a higher nesting success than younger ones, as found by other workers investigating the age of birds as a function of differential reproductive success (e.g., Coulson 1966, Mills 1973).

Cowbird Parasitism

Cowbird parasitism was a significant cause of egg loss (Table 4, Figure 6). Although other species also hosted cowbird eggs, the Clay-colored Sparrow clearly was the major host of the cowbird, with 84 out of 94 nests parasitized. Other parasitized birds on the study areas included the Western Meadowlark *(Sturnella neglecta)*, Red-winged Blackbird *(Agelaius phoeniceus)*, Brewer's Blackbird *(Euphagus cyanocephalus)*, LeConte's Sparrow *(Ammospiza lecontii)*, and Song Sparrow.

Cowbirds parasitized significantly more nests over a three-year period on Study Area 1: here 54 of 93 nests (62%) received cowbird eggs ($X^2 = 30.55$, $P<0.001$), while 30 of 139 nests (22%) were parasitized in Study Area 2. This difference correlated with the greater number of cowbirds recorded in Study Area 1 and fewer nests to parasitize. From mid-May to late June biweekly censuses of cowbirds turned up a count of 96 on Study Area 1 and 78 on Study Area 2. The incidence of parasitism declined considerably from

1974 through 1976 on Study Area 1. This decline may have been due to the cessation of cattle grazing after June 1975, allowing the vegetation to provide better concealment for the nest.

Most Clay-colored Sparrow nests that were parasitized received one (51 nests) or two (26 nests) cowbird eggs. Five nests received three eggs, two nests each contained four eggs. In all instances in which the contents of the nest were known before and after parasitism, at least one Clay-colored Sparrow egg, and occasionally two or even three eggs, disappeared, presumably removed by the female cowbird. On three occasions, one of the host's nestlings was removed and an egg substituted, a seemingly maladaptive and wasteful behavior on the part of the cowbird as in all three cases the parent sparrows were feeding young, not incubating; hence the cowbird eggs were ignored. In only one instance was a young Clay-colored Sparrow raised alongside a cowbird. In all other instances, if a cowbird was hatched and raised, it resulted in the death of the sparrow's own young.

Analysis of the response of pairs to cowbird parasitism revealed the remarkable situation that pairs on Study Area 1 generally accepted cowbird eggs while those on Study Area 2 consistently rejected them by deserting the nest (Table 5). The differences between the two areas are significant for both years combined ($X^2 = 14.78$, $P<0.001$).

Fledging

Young Clay-colored Sparrows left the nest at about nine days of age, while still incapable of flight. After hopping through the shrubbery a certain distance, they usually stopped at the base of a dense shrub, climbed it, and remained essentially motionless near its crown, waiting to be fed by their parents. The tarsus and feet of these young sparrows are well-developed, certainly large enough to support an aluminum band of adult size. It seems adaptive that advanced development of tarsi occurs in young Clay-colored Sparrows because of their high degree of mobility when leaving the nest (O'Connor 1977; Ricklefs 1969).

The distances from the nest to the selected shrub for eight young in 1976 averaged 13.6 meters ranging from 6 to 21 meters. These young represented broods from three nests, of three, three, and two young, respectively. In each case, the young dispersed radially out from the nest. The young were not clumped; rather they separated widely from each other. This radial dispersion from the nest may serve as an antipredator adaptation.

Twice I saw parent Clay-colored Sparrows move through the shrubbery with a young bird following closely behind, suggesting that adults occasionally may lead newly-fledged young away from the nest site to a safer place. The young often dispersed into an adjacent territory. On no occasion was the male holding the neighboring territory seen to show aggression towards the fledged young nor towards the parents as they flew in with food to feed the offspring. Indeed, on 21 June 1976, a male sang and preened for 20 minutes, but showed no overt agonistic behavior towards a juvenile some five meters away which had fledged from a nest in a neighboring territory. An absence of overt aggression by the territorial male persisted even though the juvenile was fed on five occasions, three times by its male parent and twice by its female parent.

TABLE 4

Categories of Causes of Mortality in Clay-colored Sparrows, 1975 and 1976 Data for Both Study Areas Combined*

Causes of mortality	*Study Area 1*	*Percentage of eggs/young*	*Percentage of losses*	*Study Area 2*	*Percentage of eggs/young*	*Percentage of losses*
Eggs laid	148			369		
Losses due to:						
Hatching failure	9	6.1	12.7	18	4.9	11.2
Cowbird parasitism	25	16.9	35.2	25	6.8	15.5
Weather & desertion	4	2.7	5.6	13	3.4	7.2
Predation	33	22.3	46.5	105	28.5	65.2
Total losses (eggs)	71	48.0	100.0	161	43.7	100.0
Young hatched	77			208		
Losses due to:						
Cowbird parasitism	2	2.6	20.0	1	0.4	1.9
Predation	8	10.4	80.0	53	25.5	98.1
Total losses (young)	10	13.0	100.0	54	25.9	100.0
Number of young fledged	67	45.3		154	41.8	

*Format after Ricklefs 1969.

Discussion

Site Tenacity

Males returning to the same territory enjoyed higher nesting success than new males. Territorial boundaries between returning males were established quickly with fewer interactions than new males.

Females exhibited a relatively low rate of return. It is likely that female Clay-colored Sparrows return to broad geographic areas, but not to the locale from which they fledged.

For those females that did return to the study areas, mate fidelity was also low. A similar situation exists in the congeneric Field Sparrow, *Spizella pusilla* (Best 1977b), but is in marked contrast to the situation in another grassland passerine, the Skylark, which exhibits 47 percent mate faithfulness in consecutive years and shows a strong correlation between the breeding success of a pair in one year and the likelihood of the pair remaining together the following year (Delius 1965).

Greenwood and Harvey (1976) point out that, in those species in which the male establishes, defends, and benefits from retaining the same territory from year to year, selection may operate for the female to disperse to a greater extent to avoid inbreeding, as in the case of the European Blackbird, *Turdus merula* (Snow 1956). Certainly establishment and maintenance of the territory is a male function in most passerines, and his fitness is apparently enhanced by retention of the same breeding territory from year to year. However, there is no evidence in Clay-colored Sparrows that females actively avoid the area in which they bred the previous year. In the Field Sparrow, Walkinshaw (*in* Bent 1968:1221) points out that the male generally accepted the first female that arrived on his territory, and he believes this to be a causal factor in the smaller return percentage of females. This is probably also the case in Clay-colored Sparrows.

Nestling Clay-colored Sparrows likewise fail to return to the nesting area. It is possible that fledglings do not form site attachments to their natal area. They wandered extensively in the late summer; one individual banded as a nestling was retrapped thirteen days later two km southwest of the study area. Also, immatures tended to collect at certain favorite locations around the study areas. Immatures of some other species, for example the Reed Warbler, *Acrocephalus scirpaceus* (Catchpole 1974), have been shown to form site attachments to specific areas in which they congregate in the fall, and to return to these areas the following spring. Such a mechanism might be operating in the Clay-colored Sparrow.

It is further possible that the preferred nesting habitat, the stands of snowberry, is not a stable one and that the selection favored a strong dispersal tendency among the young sparrows. Prairie fires were a major determinant of the distribution and composition of the vegetation in the mixed-grass prairie and aspen parkland (Bird 1961), and shrubs such as snowberry were burnt to the ground during a fire (Pelton 1953).

Territoriality

The speed with which male Clay-colored Sparrows established territorial boundaries is consistent with the observation that female Clay-colored Sparrows arrive on the average only five days after the males. The female does not appear to aid her mate in establishing or defending a territory. The situation is in contrast to that of some other open country sparrows (Potter 1972; Walkinshaw 1939; Welsh 1975) in which males arrived 20 days or more before the females, and also in which setting up a territory took much longer than in Clay-colored Sparrows.

Female arrival and subsequent pair formation coincide with a marked decrease in male aggression. Although territory size undergoes alteration after pairing in many passerines (e.g., Reed Warbler, Catchpole 1972), the situation in the Clay-colored Sparrow differs since territories, once established, did not change, and pairing and courtship both occurred without shrinkage of the territory.

Territorial defense appears to be non-existent at the time the young fledge, and neighboring males showed no overt aggression to either juveniles wandering into their territories or parents attempting to feed the juveniles.

It is not clear why pairs should have attempted second broods in 1976, but not in 1975. It is possible that the shortened breeding season in 1975 was below a threshold value needed if double-broodedness was to occur.

Nest Sites and Nesting Success

Nesting losses due to predation were greatest during the egg stage. Predators, then, did not appear to be cueing in on either the presence of nestlings in the nest or the increased activity of the parents as they fed them.

Pairs of Clay-colored Sparrows having the highest nesting success were those that selected nest sites offering a high degree of nest concealment. Most pairs appeared to minimize the chance of having their nests detected by predators hunting by sight by constructing their nests primarily in snowberry, which allowed less light penetration than other shrubs. However,

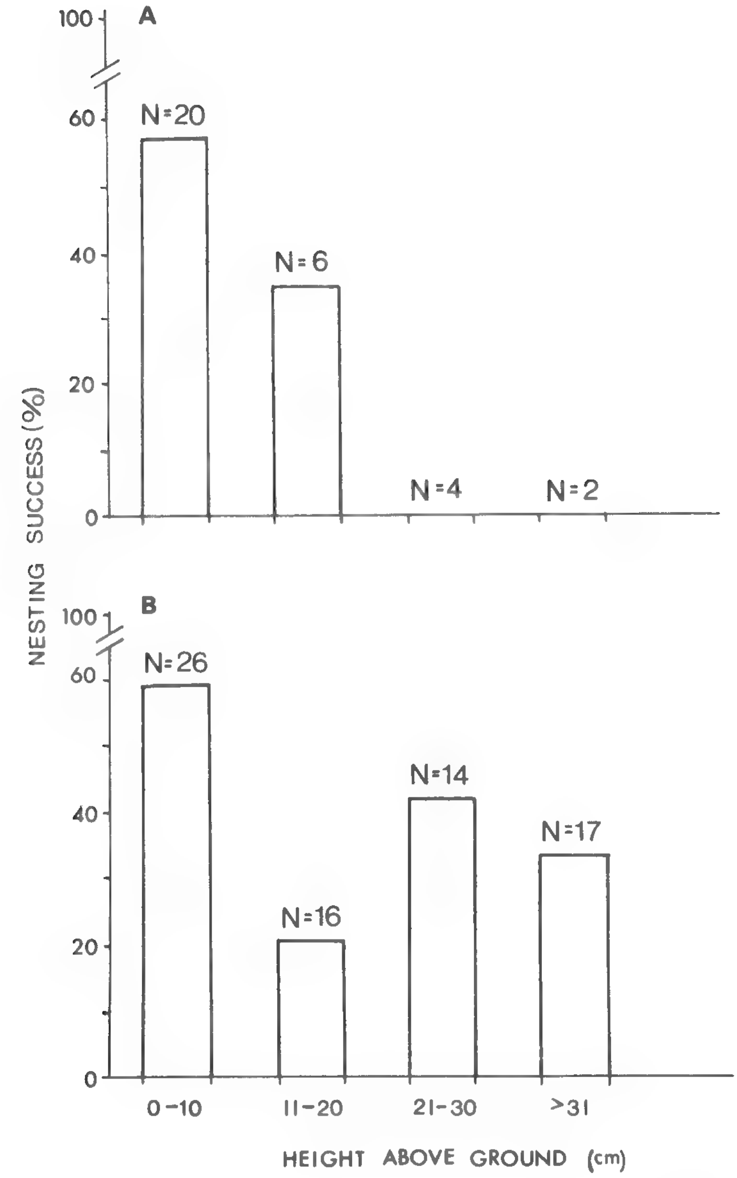


Figure 7. Relationship between nesting success and nest height in 1976. The sample included 32 nests in Study Area 1 (A) and 73 nests in Study Area 2 (B).

females may not have been selecting snowberry bushes *per se* as a nest site, but rather sites that offered a high degree of nest concealment, with snowberry offering better nest concealment than the other vegetation.

Pairs that nested close (within 10 cm) to the ground enjoyed higher rates of nesting success than those nesting higher in the vegetation. The visual outline of the nest might not have been easy to detect if the nest was close to the ground, as light penetration was less there than higher in the vegetation. Thus, it is possible that the major nest predators were ground dwelling mammals locating the nest from beneath and seeing it as a dark silhouette against the sky.

Ground squirrels were thought to be involved in nest predation on the Henslow's Sparrow, *Passerherbulus henslowii*, by Robins (1971), who noted that ground squirrels may be important predators on ground nesting birds because of their diurnal foraging behavior. Franklin's Ground Squirrel feeds omnivorously (Banfield 1974), and its depredations can be quite severe on ground nesting birds (Sowls 1948). This mammal was fairly common on both study areas in all three years of my study and may have been responsible for the loss of many nests, particularly those in which all the contents of the nest disappeared simultaneously and the nest was tipped or damaged.

Cowbird Parasitism

When Clay-colored Sparrows hatched and raised cowbird young, it almost invariably resulted in the death of the sparrow's own young. Certainly the eggs of the two species are vastly different in color and size. The sparrows' eggs are blue, sparingly marked with spots of dark brown at the large end of the egg; whereas the cowbirds' eggs are whitish and densely speckled with various shades of brown.

Rejection of the parasite's egg by removal or desertion would prevent an unnecessary channelling of the parents' energy and time into raising the cowbird at the expense of their own young. The Clay-colored Sparrow probably is not physically able to remove a cowbird's egg from its nest; therefore, the only avenue apparently open to it is desertion followed by renesting.

Rothstein (1974) classified most hosts of the cowbird into either acceptors or rejectors. Only a few species fell in the area between these two designations. Although not listed by Rothstein (1974), the Clay-colored Sparrow appears to be one such species. On a broad geographic scale, this species has been reported as incubating and/or raising cowbirds in Saskatchewan (Fox 1961), Manitoba, and North Dakota (Root, *in* Bent 1968), whereas in Alberta they are reported as being "wholly intolerant of parasitism" (Salt 1966). The birds in southwestern Manitoba appear both to reject and accept the cowbird eggs.

Although one study group (Study Area 1) contained mostly acceptors and the other (Study Area 2) consistently rejected the cowbird eggs, there is little evidence that the two populations are genetically programmed to deal with the parasite's egg in different ways. No individual banded in one study area was observed in the other, although the two areas are only 12 km apart; but there was also no evidence that young returned to their natal area to breed, a necessary requisite if gene flow between populations is to be restricted.

Individual pairs within one season were consistently either acceptors or rejectors of the parasite's egg, thus Shortt's comment (*in* Bent 1968:1194) that Clay-colored Sparrows seemed more tolerant of cowbird parasitism toward the close of the season is not borne out. Interestingly, of six females

TABLE 5

Comparison of Parasitized Nest and Host Responses in 63 Parasitized Nests of Clay-colored Sparrows on the Two Study Areas

	Number of parasitized nests	*Fate of cowbird egg*		
		Accepted	*Rejected*	*Unknown*
1975:				
Study Area 1	23	18	3	2
Study Area 2	10	2	7	1
1976:				
Study Area 1	15	8	3	4
Study Area 2	15	4	8	3

that were parasitized in both 1975 and 1976, the same four were acceptors and the same two rejectors in both years.

It is possible that effective defenses against cowbird parasitism may not have fully developed in passerine species inhabiting brush areas and forest edges. Species of the grassland edge may have been only partially exposed to the cowbird over the ages (Friedmann 1963; Mayfield 1965).

Summary

I studied the breeding ecology of two populations of Clay-colored Sparrows *(Spizella pallida)* in extreme southwestern Manitoba from 1974 through 1976. During the study, 834 birds were color banded for individual recognition.

Males showed a high rate of return from one year to the next: 45 to 60 percent on Study Area 1, 62 to 85 percent on Study Area 2. Most males returned to the same territory they had held the year before. This appears adaptive as males returning to the same territory had a higher degree of nesting success than new males. Occasionally, territorial "shuffles" occurred, in which territories were exchanged between adjacent territory holders in successive years.

Return rates of females were low, between 13 and 30 percent and, with one exception, females did not return to the same territory in successive years, regardless of nesting success. No nestling (n = 146) and only 4 of 305 immatures banded on the study areas were recorded in subsequent years.

Clay-colored Sparrows arrived on the study areas from early to middle May, with males preceding females by about one week. Males established their territories quickly, no agonistic encounters being recorded after 20 May (1976). Returning males participated in relatively few aggressive encounters among themselves, but encounters between new males and returning males, and among new males themselves, were significantly more frequent.

The mating system was monogamous. Pairs attempted to raise only one brood in 1975; but in 1976, 55 percent of the pairs attempted to raise second broods.

In 232 located nests, females laid 517 eggs and 221 young were known to fledge. Predation was the major cause of nest losses, accounting for 60 percent of the egg loss and 95 percent of the loss of young. Ground hunting mammals were thought to be the chief predators.

Pairs of Clay-colored Sparrows with the highest nesting success selected nest sites offering a high degree of nest concealment. Most pairs constructed nests in *Symphoricarpos occidentalis*, a shrub which allowed significantly less light penetration than other shrubs on the study areas. Eight-five percent of the nests were built within 30 cm of the ground, also where light penetration was less than higher in the shrubbery. Analysis of nesting success showed that nests constructed within 10 cm of the ground were more successful than those built higher in the vegetation, and that light transmission through the nest substrate was less at successful nests than at unsuccessful nests.

Brown-headed Cowbirds parasitized 84 nests. Most nests received one or two cowbird eggs; occasionally, a nest received up to four eggs. Female cowbirds removed from one to three Clay-colored Sparrow eggs in each parasitized nest. On three occasions, a nestling was removed and substituted with a cowbird egg. Pairs of Clay-colored Sparrows on Study Area 1 gener-

ally accepted cowbird eggs, while those on Study Area 2 consistently rejected them and deserted the nest.

Young Clay-colored Sparrows left the nest at about nine days of age. They were incapable of flight and moved up to 21 meters from the nest before climbing into the crown of the shrubbery, where they waited to be fed by their parents. Young dispersed radially out from the nest, often into the territory of an adjacent pair. No overt aggression was shown by territory holders to these straying young or to their parents which had to cross into a neighbor's territory to feed them.

Acknowledgments

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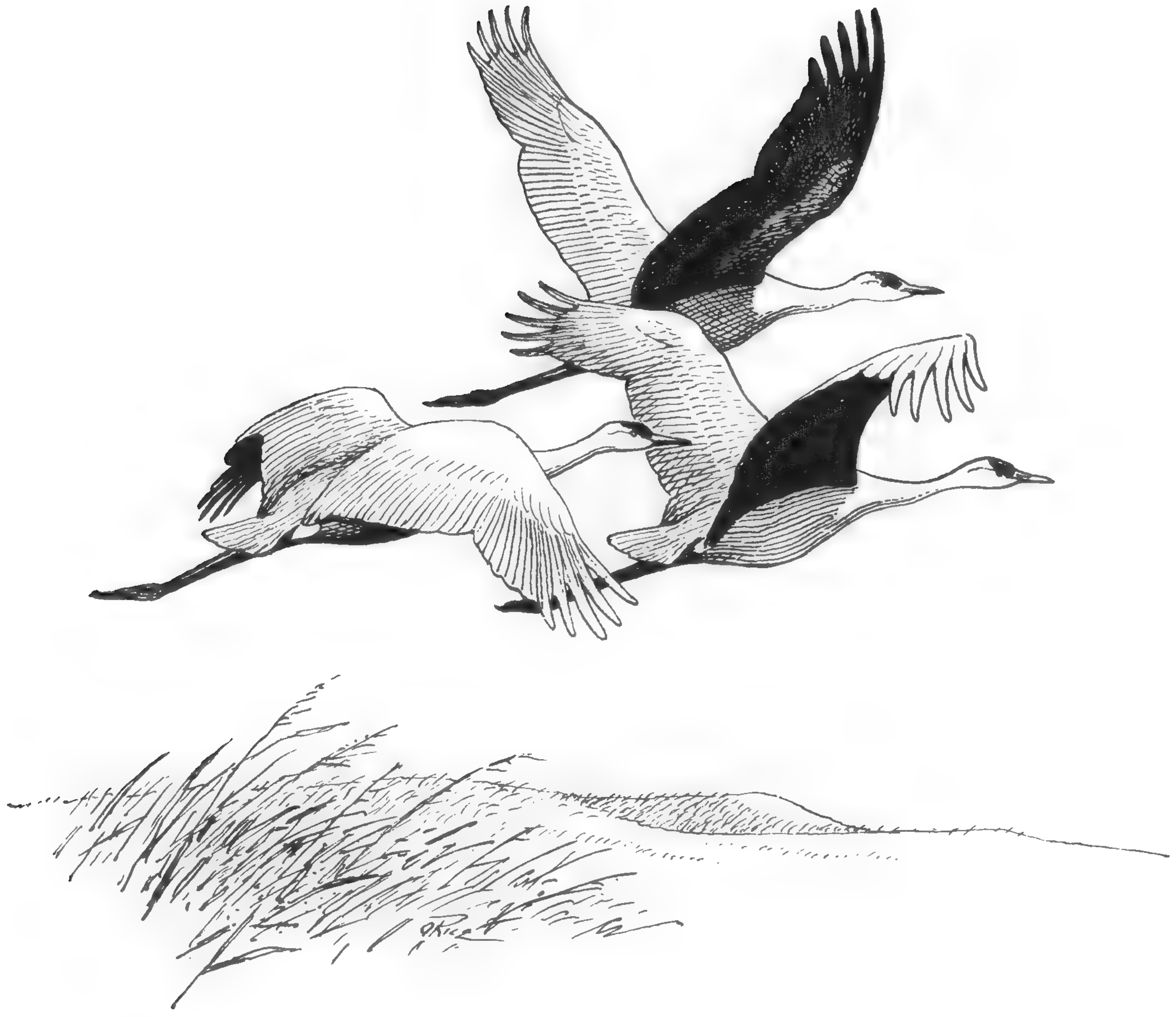

Sandhill Cranes, *Grus canadensis.* Drawing by Orville O. Rice.

THE COMMUNAL SOCIAL SYSTEM OF THE GREEN WOODHOOPOE IN KENYA

J. DAVID LIGON AND SANDRA H. LIGON

This paper is based on a continuing study of a tropical communal bird, the Green Woodhoopoe *(Phoeniculus purpureus)*, a member of the coraciiform family restricted to sub-Saharan Africa, the Phoeniculidae.

Of the six (Peters 1945) or nine (Davidson 1976) species making up the Phoeniculidae, the Green Woodhoopoe is the most common and widespread, occurring from East to West Africa, and south to the tip of South Africa (Roberts 1958). Apparently it is communal in habits throughout its range (Grimes 1975, Rowan 1970, this study). By at least some measures (e.g., abundance over large geographic areas, broad ecological tolerances), this species appears to be the most successful member of its family; thus, it does not conform to the suggestion that restricted habitat may be related to communal living (Brown 1974, Hardy 1961).

General works on African birds (Bannerman 1953, Chapin 1939, Jackson 1938, Mackworth-Praed and Grant 1957, Roberts 1958) indicate that the Green and the White-headed *(P. bollei)* Woodhoopoes are communal, that the scimitar-bills *(Rhinopomastus cyanomelas* and *R. minor)* are not, and that social systems of the Black *(P. aterrimus)* and the Forest *(P. castaneiceps)* Woodhoopoes are unknown. Our observations on *P. purpureus, P. bollei, R. cyanomelas*, and *R. minor* support these published impressions; we have not seen *P. castaneiceps* or *P. aterrimus*. This diversity of social systems within a small, rather homogeneous group is somewhat reminiscent of the genus *Aphelocoma* in the New World (Brown 1974, Hardy 1961).

Our basic goal is to reach an understanding of the ecological, behavioral, and demographic factors characterizing Green Woodhoopoes in the hope that it will provide insight into the selective forces favoring communality or cooperative breeding in this species. We hope that this, in turn, will be useful in evaluating many facets of current sociobiological theory.

Study Areas

We are studying Green Woodhoopoes at three locations near Lake Naivasha in central Kenya, at about 0°40′ S, 36°23′ E, at an elevation of approximately 1,950 meters.

Here, the woodhoopoes occupy open, flat, park-like woodland consisting of one tree species, the yellow-barked acacia, *Acacia xanthophloea*. These trees form a belt surrounding the lake. The understory is primarily grasses (Figure 1), with forbs occurring only in heavily shaded spots (Figure 2). The extremely simple vegetational characteristics of this habitat permit various parameters of the birds' environment to be readily quantified.

The three study areas are: (1) Morendat Farm, with 16 marked flocks in contiguous territories; (2) the south side of Lake Naivasha, near Crescent Island, where four flocks were banded; and (3) between the Morendat River and North Lake Road along the Naivasha-Nakuru Highway, where we banded eight flocks.

Periods of Fieldwork

This study began in late July 1975. From then until we left Kenya in mid-May 1976, we observed the woodhoopoes almost daily. We returned for the month of January in 1977 to band young birds hatched between May and December 1976 in each of the marked flocks and to record changes in flock compositions and territory dimensions. In June, July, and early August 1977, we again recorded changes in flock compositions and territorial boundaries, and made detailed observations (360 hours) at nests where familial relationships of most, or all, flock members were known. In January 1978 we banded the surviving young hatched during 1977 and obtained additional information on the marked flocks, as described above.

The long period of intensive study from July 1975 to May 1976 permitted us to become familiar with the general behavior, daily and seasonal cycles, and selective pressures, such as predators and competitors for roost sites, on Green Woodhoopoes. The shorter periods of fieldwork—January 1977, June to August 1977, January 1978—have made it possible to maintain accurate information on changes in flock compositions through time, reproductive success, kinship ties within and between flocks, and alterations in territories. Procurement of these kinds of data with periodic visits to the study area has been possible only because of the extremely sedentary nature of woodhoopoes.

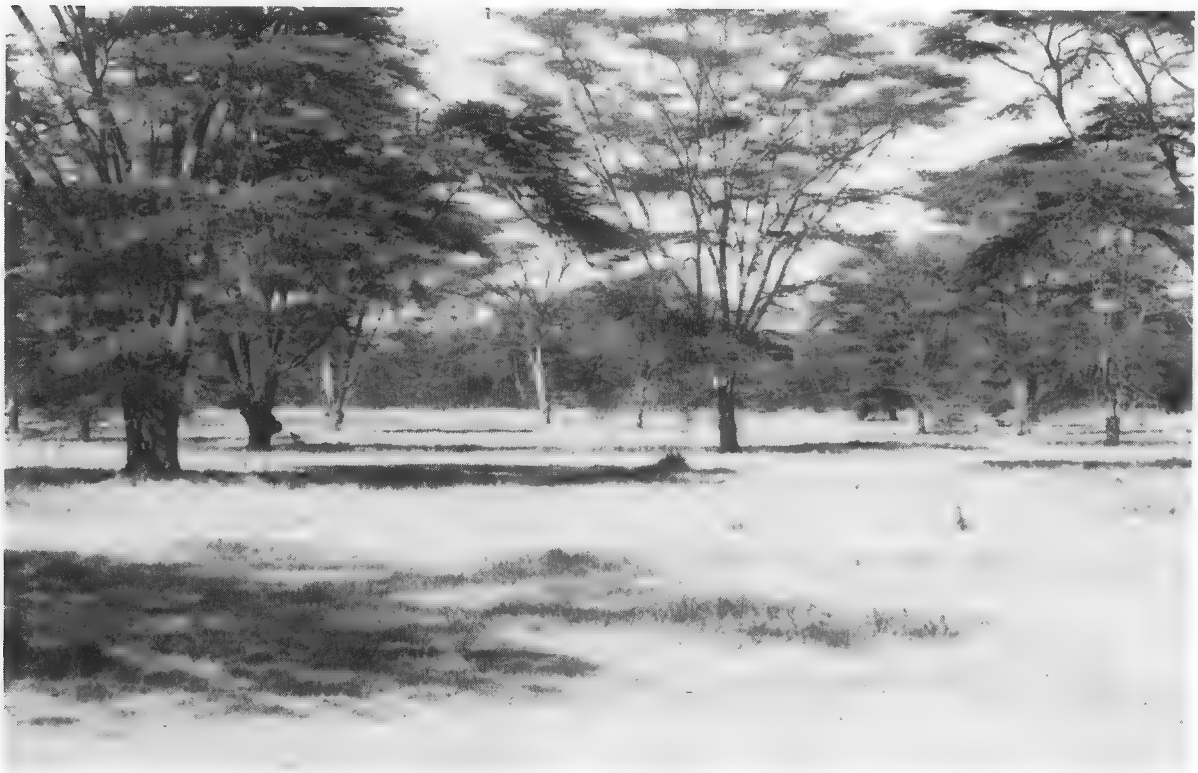

Figure 1. Open habitat of Green Woodhoopoes on Morendat Farm, near Naivasha, Kenya. Photograph taken in January 1979. Trees are the yellow-barked acacia *(Acacia xanthophloea)*. Grasses are the primary ground cover.

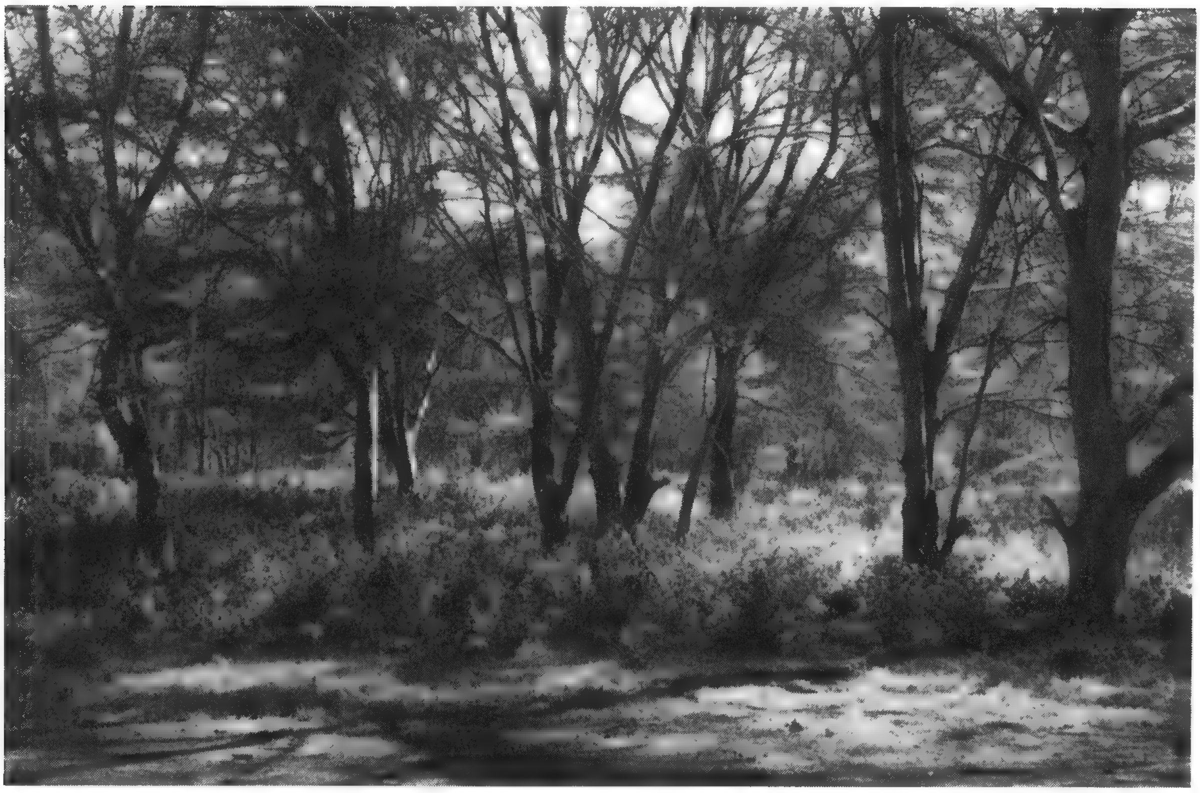

Figure 2. Shaded area with dense undergrowth on Morendat Farm. Taken in January 1979.

Methods

To study the social behavior of Green Woodhoopoes and to learn the role of each individual in a given flock required individual marking of birds. Since mid-1975, we have banded a total of 235 woodhoopoes in 28 flocks. The fact that woodhoopoes roost in cavities greatly facilitated their capture. After dark, one of us climbed to roost cavities, which contained from one to seven birds, and plugged them. Early the following morning, a clear plastic bag was tacked over the entrance, the plug removed, and the birds allowed to emerge from the cavity into the bag. Often this was triggered by taped playback of woodhoopoe vocalizations. The other major means of capture was by use of mist nets and a tethered woodhoopoe. We occasionally placed a tethered adult on a stump positioned inside the base of a "V" formed by two nets, then played a tape of woodhoopoe vocalizations. When the territory owners discovered such an "intruder," they generally attacked it, and some became entangled in the nets.

In most flocks all individuals were marked by a single colored plastic band and by a uniquely numbered, aluminum ring provided by the East African Natural History Society. When uncertainty arose concerning the identity of a banded woodhoopoe, the bird was recaptured.

When individuals of any species of bird disappear, one seldom can be certain of their fate. However, for several reasons we feel that the disappearance of Green Woodhoopoes in most cases meant that the bird had died. In the first place, since the beginning of the study in 1975, no breeding bird is known to have left its original territory, with two exceptions. Each of these moved to an adjacent territory where breeding vacancies were available because of the disappearance of males. Secondly, the remains of several banded birds noted as having "disappeared" subsequently were found (see section on Predation and Mortality). Thirdly, all non-breeding males that left the territory in which they were originally banded moved into a portion of the parental territory (also see Woolfenden and Fitzpatrick 1978), or into an immediately adjacent territory, almost always in groups of two or three. These movements are described under "Emigration, Immigration, and the Formation of New Social Units." Despite a careful search with the aid of taped vocalizations, we never have recorded a banded bird in areas adjacent to the study sites. Adult, non-breeding female woodhoopoes, as in some other communal species (e.g., Woolfenden 1973, 1975; Zahavi 1974), are more prone to move about than are males. However, like male emigrants, they usually emigrate as small groups into an adjacent territory. Our evidence thus indicates that movement by breeders, juveniles, and male helpers is very conservative. Therefore, we conclude that most birds that cannot be located probably have died.

One other major point critical to development of an understanding of kinship and behavioral relationships within and between flocks is knowledge of parentage of young birds (see section on Breeding).

Flock Compositions

Size of Flocks

Stable social units of Green Woodhoopoes range in size from a single pair to 17 birds (Figure 3). We counted most of 28 marked groups at six-month intervals from July 1975 through January 1978, yielding 130 flock counts. Overall, mean flock size was 5.62 birds. Extremes of two or greater than nine were uncommon. About 92 percent of the flocks ranged from three to nine with 38 percent numbering either five or six.

The rarity of flocks of more than nine suggests that they might be at some selective disadvantage. However, a flock sometimes far exceeds the norm for a period of time. For example, one flock (DD) increased from nine to 16 birds during the latter half of 1975, entirely by producing young. In May 1976, at the onset of the annual breeding cycle, this flock contained 15 birds; however, their reproductive success in 1976 was very low, for unknown reasons, with only one juvenile surviving until January 1977. During January, the juvenile and the breeding male were taken by predators. By June 1977 all but two members (original breeding female and one daughter) of the 15 birds comprising the flock in May 1976 had either emigrated from this territory or died. However, the original breeding pair had been highly successful in that, as of July 1977, their offspring occupied breeding positions in four of seven contiguous flocks.

Sex Ratio

The sex ratio in woodhoopoes is usually equal overall, but either males or females or neither may predominate in a given flock. In contrast, numerical superiority of males apparently is common in many communal breeders (Fry 1972; Rowley 1965; Woolfenden 1975, 1976). This has been attributed to the fact that females leave the natal territory earlier and more frequently than do males, and are thus exposed to greater predation (Rowley 1965, Woolfenden 1975). Woolfenden and Fitzpatrick (1978) suggest that male helpers in Florida Scrub Jays *(Aphelocoma c. coerulescens)* frequently gain breeding space by remaining at home and "inheriting" a portion of their parents' territory, whereas females must leave the natal territory and locate a vacancy elsewhere to obtain breeding status. Such female-biased dispersal also occurs to some extent in Green Woodhoopoes; however, in this species females also parallel all male patterns of territorial acquisition, including inheritance of the territory.

Sexual Dimorphism and Age Variation

In many communal species, sexual dimorphism is slight and often conspicuously less than in non-communal congeners (Brown 1978; Ligon 1970 and unpubl. MS). However, Green Woodhoopoes exhibit considerable sexual dimorphism in body size and in vocalizations. Males are larger than females. Fifty-nine males ranged from 69 to 97 grams with a mean of 77.8 grams; sixty females ranged from 52 to 75 grams with a mean of 64.3 grams. The mean bill length of 52 males was 49.9 millimeters (range 45 to 55 millimeters); bill length of 53 females was 39.7 millimeters (range 36 to 44.5 millimeters). These differences are highly significant (Student's t, $P<0.001$). The weights used here are of birds captured at various times of the day—at dawn before foraging and at midday after extensive feeding. Bill lengths showed no overlap (Figure 4).

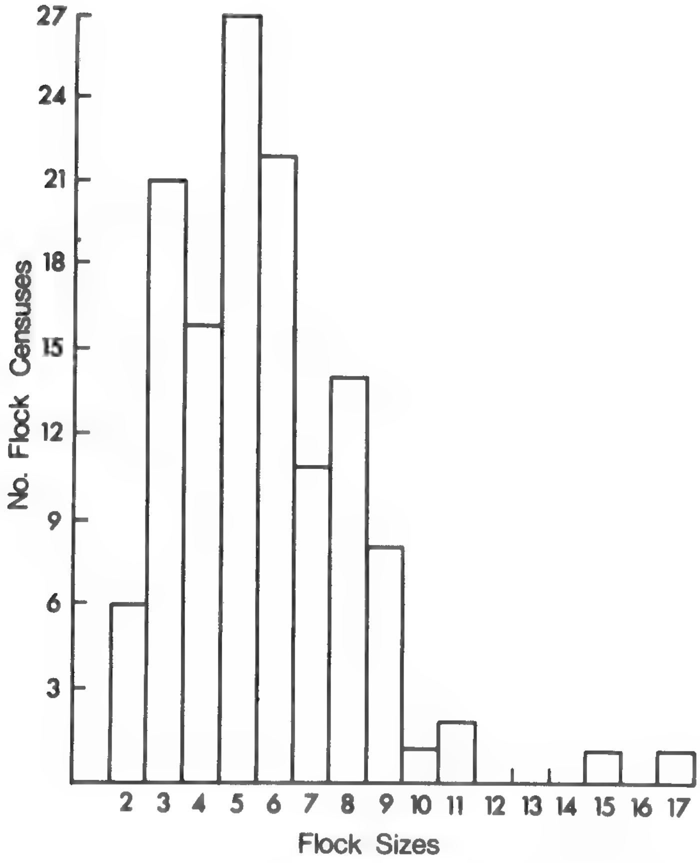

Figure 3. The size of marked groups at six-month intervals. Most of the social units (92 percent) varied from three to nine birds.

To our knowledge all vocalizations of adult woodhoopoes are sexually diagnostic. This is unusual and the adaptive significance of such differences is not altogether clear.

At fledging, juvenile woodhoopoes have black bills. Juvenile males also often have brown throats, whereas young females rarely show this trait. Size dimorphism is well developed prior to fledging and this, together with the sexual differences in throat color and possibly vocalizations, probably serve to identify the sex of young birds and may make them individually recognizable as well.

Bills of immature woodhoopoes change from black to red over the first year or more of their lives. This change is gradual and predictable, allowing us to recognize juveniles from first and second broods. This change possibly provides an additional means of individual recognition. Such change in bill color and/or other morphological characteristics is a common feature of communal birds. Many of the communal New World jays, in particular, show striking age-based variation in bill color, eye color, etc. (Hardy 1973). As a result, in many communal groups almost all members are individually recognizable to the human observer, and presumably to the birds as well. The sexual differences mentioned above further emphasize individual variation. Thus, visual recognition alone may be sufficient to maintain individualized social interactions within woodhoopoe groups. In the communal Acorn Woodpecker *(Melanerpes formicivorous)*, flock members are said to attack outsiders on sight even when the latter have not vocalized (MacRoberts and MacRoberts 1976).

Changes in Flock Size and Format

Woodhoopoe flocks are nearly closed social units so long as both members of a reproductively successful pair remain alive. We have recorded almost no immigration of new birds into such flocks. Woodhoopoes of each sex generally move into a new area only if conditions favor formation of a new social unit, or if a breeding vacancy occurs in an adjacent territory.

An emigrating unit usually consists of two or three woodhoopoes of the same sex; often these are siblings. Typically, these groups move no farther than to an adjacent territory (Figure 5). Emigrating siblings usually are of different ages, with the eldest becoming the new breeder in the newly formed or reconstituted flock. This pattern of movement often leads to social units consisting of brothers and some related females (sisters, mother and daughter(s), etc.), or vice versa. Such movement into a new territory by unisexual groups appears to be adaptive in that two or more individuals are more likely to succeed in competition for flock ownership than is a single bird and are also more likely to resist encroachment and aggression by neighboring flocks.

For example, in one case a lone male (OR) moved into an adjacent territory (3S) to join three females soon after their two male flock-mates had died. This male (OR) remained with the females in their territory for about a month before three sibling males from another nearby flock (KG) moved into the territory and drove out the lone male (OR), who returned to his original flock. Following their entrance into the territory (3S), the three males, along with the three females, conspicuously and successfully engaged surrounding flocks in territorial encounters. That is, this group of six apparently had sufficient numerical strength to hold and perhaps expand territorial boundaries against neighboring groups that had encroached on the 3S territory following the deaths of the two original males.

In nine instances unrelated birds of the same sex merged to form a new or renewed flock. In seven of these, one or two females joined two older

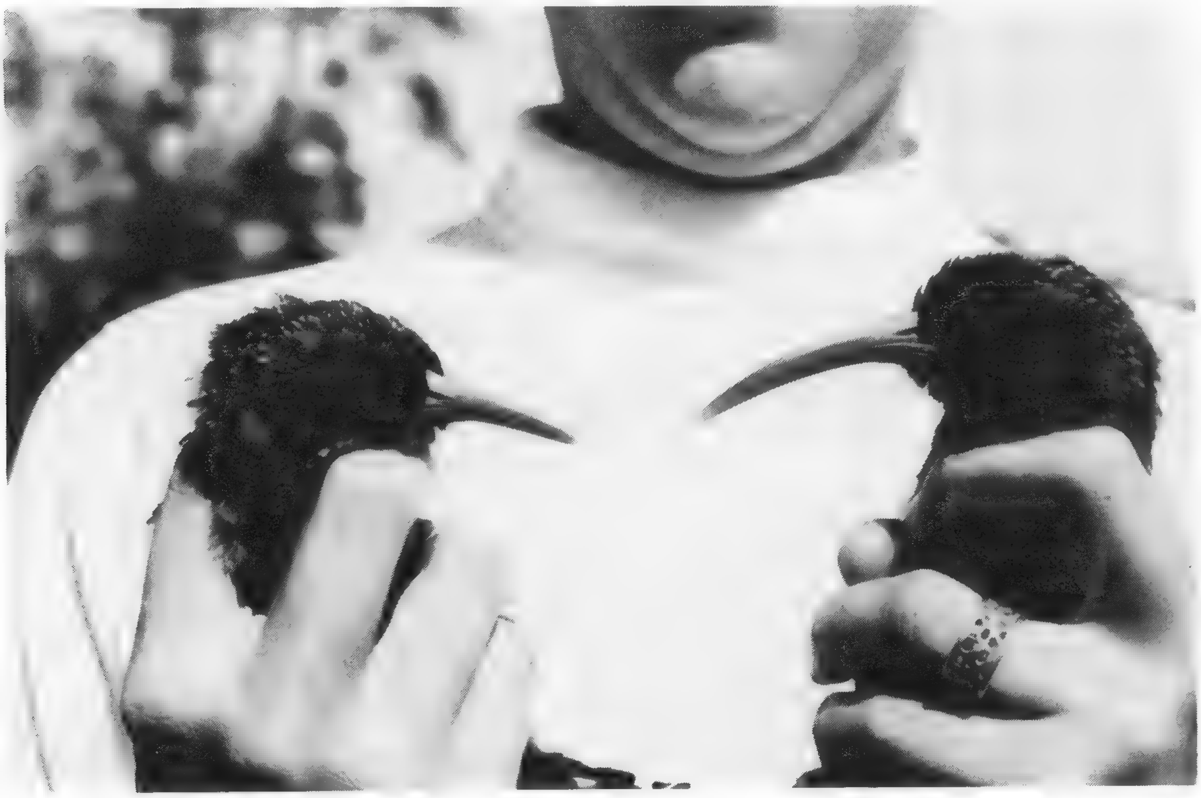

Figure 4. Adult male (right) and female Green Woodhoopoes, illustrating sexual dimorphism in bill lengths.

females. Our data suggest that the original, older females were sisters. Twice a young male joined a new flock containing one male and two and three females who very weakly defended a small territory. These few records suggest that acceptance of outsiders is restricted to newly forming social units whose potential breeders can directly benefit by the addition of subordinate members. This benefit seems to be most directly related to the increased ability of larger flocks to defend space. By accepting recruits, small groups of three to four gain by the increased stability and defense of their territories.

When a breeder of either sex dies, the cohesion of a flock, particularly a large stable one, is destroyed, apparently because such flocks are composed of parents and their offspring, and inbreeding between parents and young, or between siblings, is avoided. For example, the female breeder in Flock RF died, leaving a small nestling. The remainder of the flock, four males and two females, reared the young female. Prior to the next breeding period, this flock of seven dispossessed a small adjacent group of four and the four males of Flock RF then left the original territory and moved into the newly acquired space. The three females remained on the original territory and were joined by a male from a neighboring flock. The departure of the males is puzzling, in that they surely could have remained in their first territory and expelled the females. Perhaps the new territory offered superior roosting sites or other resources. Their ability to take the territory may have been due to some calamity to original occupants, leaving the territory weakly defended. In another flock, both breeders died within a few weeks of each other, leaving three females and three male offspring. Again it was the males that left, joining their brothers in a nearby flock, while the females remained and were joined by four males from a large neighboring flock.

To sum up, non-breeding adult woodhoopoes typically leave their original flock in the parental territory and transfer in unisexual groups of two or three only when an opening occurs in a nearby flock. Sometimes females also disperse without having a territory to enter; such females sometimes merge to form a new social unit. This apparently never occurs in long-established groups. In the small new flocks such "recruits" aid the established flock members by participating in territorial defense and by feeding young produced by the breeding pair (Ligon and Ligon, 1978). Death of a breeder of either sex usually terminates flock stability for a time unless a sibling of the deceased breeder is present, in which case it assumes the role of breeder.

Kinship Ties within Flocks

In each flock of Green Woodhoopoes, regardless of its size, only one breeding pair exists. The pair is essentially monogamous and they are the only reproductives in the group. The male breeder is almost always the oldest male in the flock, and the female breeder usually is the oldest member of her sex; however, exceptions to this latter generalization occasionally occur (see Section on Mate Choice and Pair Bond).

Other flock members usually are male siblings of the male breeder, female siblings of the female breeder or, in flocks where the pair remained alive for one or more years, offspring of the breeding pair. This last category makes up the great majority of the membership of at least some larger flocks. In addition, nieces and nephews of breeders occur in those flocks where the original breeding male or female died and was replaced by a sibling. A grandmother lived in one flock. Thus, family ties generally are close. However, in some flocks we studied, birds unrelated to either breeder occur; they behave as integrated group members, aiding in territorial defense and feeding young. These units illustrate that family ties, although usually present, are not an invariable aspect of woodhoopoe sociality.

To sum up, our data indicate that flock members are usually, but not always, close genetic relatives of at least one of the breeding birds. It also appears that small, unestablished groups are more likely to accept "outsiders" than are larger, established social units. This is highly adaptive in that establishment and maintenance of territory require numerical strength. The dominant birds, which will breed if a territory is established, gain by the presence of other, subordinate individuals. The younger, subordinate birds likewise gain by this arrangement in that they will have a secure territory in which to roost and forage; moreover, if the dominant individual(s) of their sex die, the younger birds will attain breeding status in an established territory and will acquire the immature offspring of the previous breeders as nest helpers or provisioners for their own offspring, whether or not genetic ties exist (Ligon and Ligon 1978).

General Behavior

The daily activity patterns of woodhoopoe flocks vary little during the non-breeding period. The birds pass most of the day moving through their territories, foraging, exploring cavities and crevices in trees, loafing, allopreening, or engaging in territorial activities. Here we briefly describe some common behaviors.

Foraging

Green Woodhoopoes are rather specialized morphologically, apparently in part as the result of selective pressures related to foraging. The bill is long, slender, and decurved in males; tarsi are short and thick, and toes strong; and the long tail is used as a prop. All of these characters are related to feeding on the trunks, limbs, and branches of trees, by probing cracks and crevices, and by using the bill to investigate wads of old spider webs and frass.

In addition to foraging on tree trunks and large limbs, woodhoopoes use terminal branches and twigs, and often, especially during the dry season, they forage on the ground, probing and tearing apart cow manure. They also hawk flying termites when these insects engage in their mass nuptial flights. Thus, despite their specialized appearance, woodhoopoes have a broad repertoire of feeding behaviors.

Dominance and Aggression

A flock of woodhoopoes appears at first to be a highly integrated, cooperative unit. However, agonistic encounters and dominance-subordinate relationships are frequent enough so that in many cases we could assign dominance rankings. Males dominate females, and older birds dominate younger ones of the same sex, as was found for Florida Scrub Jays by Woolfenden and Fitzpatrick (1977). The breeding (alpha) male is dominant, yet this bird frequently performs behavior that appears to "appease" other male flock members, especially after the alpha male has threatened or supplanted a secondary male (see section on Paternity). In June to August

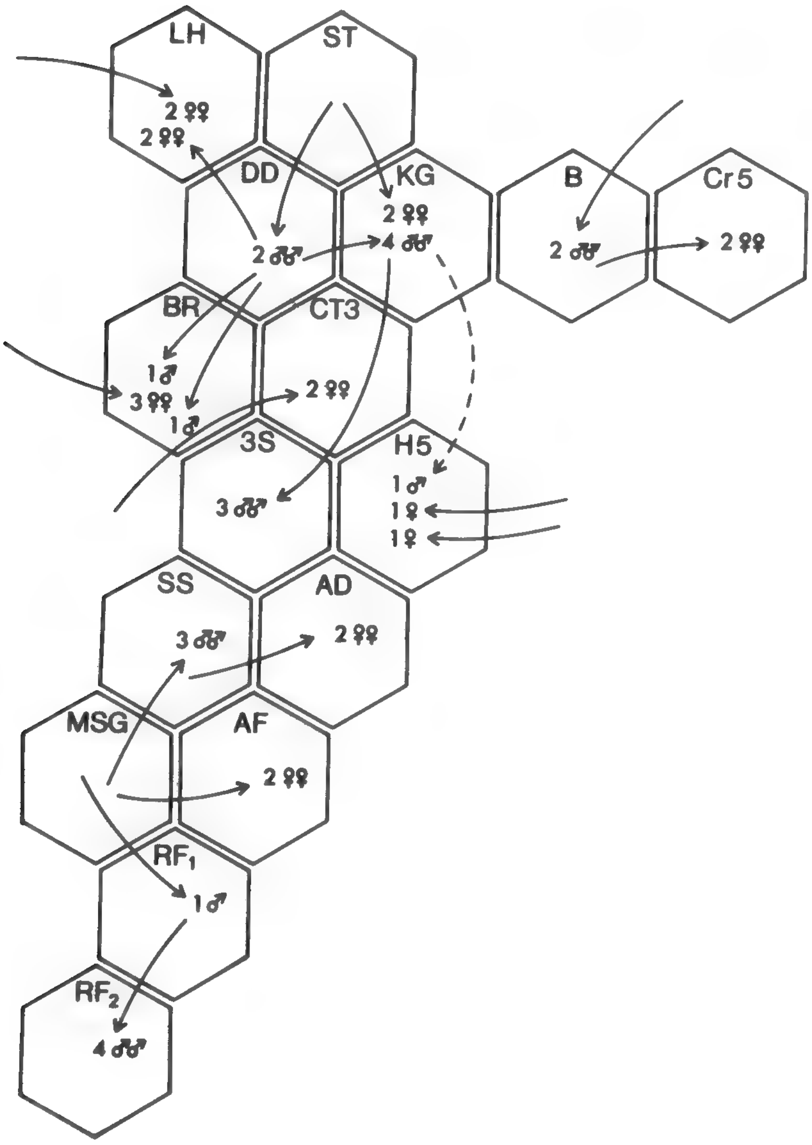

Figure 5. Movement of Green Woodhoopoes from one territory to another. Hexagons represent territories, letters identify each territory, arrows indicate the direction of movement, and the number and sex symbols at the arrowheads indicate the composition of the immigrants. For example, three males moved together from the MSG territory to the SS territory; earlier, and independent of that immigration, two females moved from the SS territory to the AD territory.

1977, soon after many flocks had undergone major reorganization, intraflock aggression appeared to be considerably higher than in 1975. We attribute this to differences in flock compositions in the two years. In 1975 several of the flocks we watched most closely were large and probably consisted mainly of parents and their grown offspring; in those flocks aggression was low. In contrast, many flocks in 1977 were made up of adult sibling groups and/or unrelated birds. In these flocks, potential competition for mates and breeding status, or at least matings, was present, and aggression between flock mates was higher than in 1975.

Allopreening

In woodhoopoes, allopreening is an important intra-group behavior, as it is in many other communal breeders (Brown 1978). Gaston (1977) has shown that allopreening and dominance are related in Jungle Babblers *(Turdoides striatus)*. This may be true to some extent in woodhoopoes as well, for older birds tend to groom younger ones. In addition, however, females frequently groom males, and dominant and subordinate males take turns grooming each other, as do females. Thus, the role of allopreening in woodhoopoe sociality is more complex than a subtle assertion of dominance (Harrison 1965).

In addition to a social role, allopreening very likely is of more direct significance. We have often seen eggs of bird lice on feathers of the nape and head as we handled woodhoopoes. Moreover, at two nests the young died after infestation by mites. Thus, a functional basis for allopreening exists apart from its social significance.

Rallies

Jackson (1938) was one of the first writers to describe what we term the Rally Display: "On assembling together, after a short flight from one tree to another, it (woodhoopoes) is much given to a loud, excitable and tippling chatter, all the birds calling together in chorus as they sway their bodies from side to side and their tails up and down in a ridiculously quaint fashion. This chattering can be heard at long distances. ... " This description emphasizes that the display is a group activity consisting both of loud vocalizations and exaggerated movements of the body. The rally is an intraflock activity that serves, we believe, to promote flock unity and cohesion. Rallies are most intense during territorial encounters between flocks; they also occur when flock members are reunited. For example, birds released after having been captured for marking are greeted with a Rally Display by other flock members.

Territoriality

Green Woodhoopoes, like most other communal species, are both highly sedentary and highly territorial. Territorial activities—defense or intrusion—typically occur several times a day. Frequent interactions with neighboring flocks provide individual woodhoopoes with continuing information on changes in the composition of adjacent groups and thus makes possible rapid exploitation of a breeding vacancy. In January 1977 we captured the female members of the Flock Cr and within an hour or so three females from the adjacent Flock SS had entered the territory held by Flock Cr and had begun interacting with the sole adult male. Apparently the absence of the Cr females had notified the SS females of vacancy. A year later a similar incident occurred when the Cr females were again captured. Two females from another adjacent territory promptly joined the two Cr males. Clearly, females from adjacent flocks sought to occupy the Cr territory as soon as it appeared that the original females were gone.

An important aspect of flock size in woodhoopoes is the relationship between numbers and territorial incursion and defense. Larger flocks can intrude into the territories of small groups, and the greater the disparity in group sizes, the more difficult it is for small units to resist larger ones. Flock DD numbered 15 birds from January to May 1976 and penetrated deeply into all surrounding territories with near impunity. This increased opportunity to exploit resources over large areas may be a major advantage of being a member of a larger flock when food is scarce or is patchy or unpredictably distributed in time or space. Our observations suggest that insects often are clumped, especially during the dry season; thus, freedom of movement of large flocks may compensate for the increased number of individuals foraging together. In any case, Flock DD ranged into surrounding territories and appeared to thrive during the dry period from January to April 1976.

In short, although territories are vigorously defended and boundaries well known to the birds, trespassing is common, and members of larger groups are more successful in invading adjacent territories and in resisting intrusions than are small flocks.

Flag-waving

Intraflock unity appears to be pronounced during territorial encounters. This is not surprising because every flock member has a direct stake in defending the territory and expelling intruders. A common, but peculiar, display exhibited by woodhoopoes usually is seen during interflock territorial encounters; we refer to it as Flag-waving. It occurs just prior to a territorial confrontation, but after the home flock is aware of the presence of intruders. One or two individuals, usually including at least one member of the breeding pair, pick up in the tip of the bill a clump of lichens, a piece of bark, or a wad of spider web and frass and wave it vigorously back and forth. These individuals then usually fly toward the intruders ahead of the rest of the group. When the two flocks confront each other, members of each one clump tightly, give vigorous rally calls in unison, and rock back and forth with the wings partially extended and the tail fanned. Flag-wavers tend to position themselves in front of their flock and closest to the opposing group, and to thrust the "flag" toward the other group, which may be only a few feet away. Often the defending group passes the flag back and forth between several individuals. Prior to and during these territorial fights, males give low growls, a vocalization indicative of aggression (Morton 1977).

It appears to us that Flag-waving serves to incite other flock members and perhaps enhances coordination in aggressive defense. If flocks are of about equal sizes, the defenders successfully deter the intruding group, either by the intensity of their display or, if that fails, by direct attacks. MacRoberts and MacRoberts (1976) describe "waka" displays in communal groups of Acorn Woodpeckers that appear to serve, in part, the same functions as those of flock Rallies and Flag-waving in the woodhoopoes; namely, they increase intragroup cohesion and perhaps incite concerted aggression by the group.

We also have observed woodhoopoes carrying flags in other, nonterritorial contexts. For example, when mobbing a potential predator, flock members gather near it and give short, sharp alarm calls. Typically, the birds approach the predator with caution. Some individuals display more aggressively than others, arching the neck, drooping the wings, and fanning the tail while swaying back and forth, as in territorial encounters. Often, the bolder woodhoopoes carry flags, waving them as they sway before the predator. Here, too, the flag may be passed among several birds. However, unlike territorial rallies, we saw black-billed juveniles participate in these displays. Most such displays were directed toward Gabar Goshawks *(Melierax gabar)*, but other avian predators, such as Augur Buzzards *(Buteo rufofuscus)*, Peregrine Falcons *(Falco peregrinus)*, Harrier Hawks *(Polyboroides typus)*, Fishing Eagles *(Haliaeetus vocifer)*, and Tawny Eagles *(Aquila repax)* are mobbed in a similar fashion. The woodhoopoes also mob large-spotted genets *(Genetta tigrina)* that they find in cavities in trees.

The woodhoopoes used flags in two other contexts. Once, a female parent displayed aggressively on her nest snag toward Blue-eared Glossy

Starlings *(Lamprotornis chalybaeus)*. She carried a lichen flag and swaggered about with full aggressive postures. These starlings are severe competitors of woodhoopoes for cavities. Another incident involved newly fledged young. As a juvenile, out of the nest for two days, pecked about on the ground with the flock foraging nearby, an adult female helper picked up a piece of lichen, flew to the young, positioned herself in front of it, and engaged in a bowing rally display. She then passed the lichen to the fledgling, who soon dropped it.

Interspecific Interactions

Competition for Roost and Nest Sites

The most conspicuous and common kind of interspecific interaction involving Green Woodhoopoes is competition at roost and nest sites. Cavities suitable for roosting and nesting apparently are scarce and are used by a number of birds, as well as other animals; as a result, competition for this resource is intense. The most frequent bird competitor of the woodhoopoe is the pugnacious Blue-eared Glossy Starling. Aggression between woodhoopoes and these starlings is commonly seen as supplantings, short flights at one another, and some physical contact. In contrast, the large and highly aerial Lilac-breasted Rollers *(Coracias caudata)* clearly dominate woodhoopoes on most occasions. We saw groups of woodhoopoes forced from the air into the cover of thick growths of acacia twigs. One flock of six woodhoopoes was harassed almost continually as they attempted to provision small nestlings. Although the rollers had an active nest nearby, they vigorously "defended" the woodhoopoes' nest hole from the owners. The woodhoopoes, after being driven into a thorn thicket, perched quietly for a time. Shortly, one or two birds began to approach the roller by hopping cautiously up the branches to where the roller perched. These woodhoopoes then opened their wings, sleeked the contour feathers, extended their heads, and swayed slowly and rhythmically back and forth in an unusual serpentine manner. This display sometimes resulted in the supplanting of the roller. The interactions of this flock with the rollers illustrate one benefit of group living. By approaching the nest tree and advancing as a group, some individuals reached the nest with food for the young, because the roller could direct its aggression toward only one or two woodhoopoes at a time. The young were reared successfully.

Occasionally woodhoopoes also behaved aggressively toward Superb Starlings *(Spreo superbus)*, primarily at nest holes, although this species is not a regular hole user. Green Woodhoopoes are dominant over two other locally common hole nesters, the Grey Woodpecker *(Mesopicos goertae)*, which excavates most nest holes used by woodhoopoes, and the Hoopoe *(Upupa epops)*. Woodhoopoes supplant both species from roost and nest sites. Acacia rats *(Thallomys paedulcus)* are abundant in our study areas. These arboreal rodents sometimes drive woodhoopoes from roosts at dusk and sometimes occupy woodhoopoe roosts.

Although we have not observed conflict between woodhoopoes and the following species, all are common in our study areas and use similar-sized cavities: Striped Kingfishers *(Halcyon chelicuti)*, Bearded Woodpeckers *(Thripias namaquus)*, Nubian Woodpeckers *(Campethera nubica)*, and Pearl-spotted Owlets *(Glaucidium perlatum)*.

Another major competitor for holes against which woodhoopoes have no defense is the African Honeybee *(Apis mellifera)*. This insect is conspicuously abundant in the open acacia woodland. The bees swarm frequently during the dry season, searching for suitable hive sites. Five roosts of our marked flocks have been taken over by bees.

Green Woodhoopoes also mob potential predators (see section on Flag-waving) and actively pursue parasitic honeyguides *(Indicator indicator* and possibly *I. minor)*, vigorously chasing them away from nests.

Predation and Mortality

Mortality is high and unpredictable in Green Woodhoopoes and this may have profoundly affected the evolution of the social system in this species. Over a two-year period, January 1976 to January 1978, we recorded a mean annual survivorship of about 40 percent in all categories of age, sex, and social status (Ligon, in press). These data indicate that every woodhoopoe faces a rather high probability of dying during the following year.

Nocturnal Predation

What are the nocturnal predators? We believe that cats, both wild and feral (*Felis libyca* and *F. domesticus*, respectively), the large-spotted genet, and possibly slender mongooses *(Herpestes sanguineus)* are responsible for most nocturnal mortality. Cats and genets are common on our study areas and we have seen both frequently in trees at night. Nocturnal arboreal hunting should be attractive to such predators not only because woodhoopoes and other birds roost in cavities, but also because acacia rats are abundant and are active at night.

Woodhoopoes invariably roost in cavities in trees or, when cavities are unavailable, under bark. We have never seen a woodhoopoe roost in an exposed place, despite having watched birds go to roost hundreds of times. This absolute aversion to roosting in apparently safe, open sites such as thick, thorn-covered branches of acacias is puzzling to us, because the birds are easily captured from some cavities, and this appears to be where predation is most common. Perhaps woodhoopoes are unable to remain endothermic in the absence of insulation afforded by the roost. We hope to explore this possibility, and others, in future research.

Most evidence that woodhoopoes are preyed upon at roost sites is circumstantial. For example, birds in good standing in the flock often abruptly disappear; sometimes two or more disappear at the same time. As these birds often roost in groups, it seems likely that they met the same fate, although we usually discovered no hard evidence to account for their fate. However, in three cases we documented nocturnal predation.

In early 1976 Africans chopped down several large trees in two territories to make charcoal. Large, old trees were scarce in these territories and some of those cut apparently had been vital roost trees for the resident flocks. One group numbered three in March, two in May, and was gone by January 1977. Other groups have not appeared in this unoccupied territory. In May 1976 the five members of the other flock flew two kilometers across treeless grassland twice a day to an isolated roost tree in late afternoon, and back to the territory the next morning. The risks involved in flying across open country undoubtedly are great, attesting to the overriding importance of roost sites. All of these birds disappeared by January 1977. Five unbanded birds appeared. These we captured with mist nets and banded. By June 1977, they too had disappeared and were replaced by an unbanded pair. The

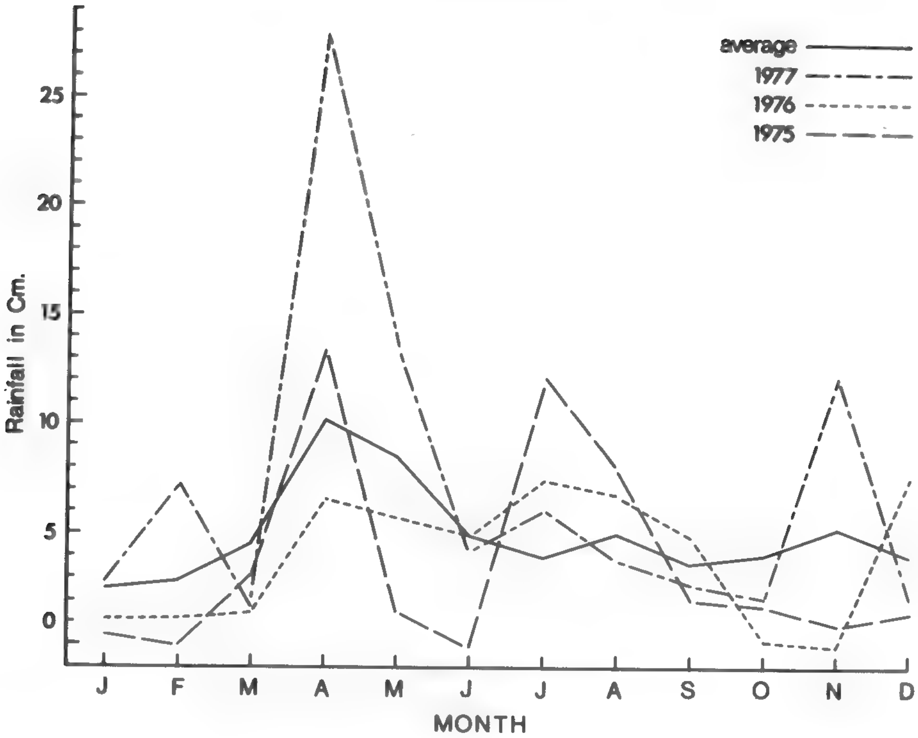

Figure 6. Monthly rainfall over three years of the study, 1976 through 1978. The solid line represents a 34-year average, 1934 to 1968.

latter were gone by early August. Thus, within a few months, members of each of these groups either died or vacated what appeared to be high quality habitat, probably because of the absence of adequate roost cavities.

Between 1 February and 1 June 1977 mortality was almost four times higher than during an approximately equal interval from mid-January to mid-May 1976 (26% vs. 7%). We believe that this high mortality was caused primarily by the extraordinary rainfall of April 1977 (Figure 6) and the effect it had on roost sites. Heavy rains can fill roost cavities, forcing the birds to roost in more vulnerable spots, for example, under bark. In June the posterior half of one woodhoopoe, including the rectrices and the distal portions of the remiges, was bleached, with an abrupt transition between the lightened feathers and the unaltered plumage. Apparently this bird had perched vertically inside a cavity that had partially filled with water containing compounds from the acacia tree, causing the change in feather color.

Other Sources of Mortality

Woodhoopoes also must contend with several diurnal birds of prey. A young woodhoopoe was lost on the day it fledged, almost surely to a Gabar Goshawk. We observed this flock with the two surviving fledglings for several days thereafter. The woodhoopoes were followed almost continuously by a family of these hawks. However, because of the alertness and aggressiveness of the 14 older members of the flock, the other two young birds survived to independence. Although Gabar Goshawks are probably the main predators of flying young, Harrier Hawks pose a threat to incubating females and/or nestlings. This hawk is a hole-probing specialist, much like the Blackish Crane-hawk *(Geranospiza nigra)* of Central America (Jehl 1968). A Harrier Hawk was seen regularly in the vicinity of a nest where one small nestling died in October as a result of a single deep puncture in the body. We suspect the hawk reached the nestling with the tip of a talon, but was unable to grasp and remove it. In another flock, the incubating female left the nest cavity quickly and silently as a Harrier Hawk flew to it; as no other woodhoopoes were present to give alarm calls she probably was responding to its specific flight sounds. Augur Buzzards also apparently prey on woodhoopoes. On one occasion we had tethered a bird to a fencepost and placed mist nets around it, in an effort to capture others. An Auger Buzzard came in at high speed, going right through the nets. Despite the nets and our shouts, it came back twice more (unsuccessfully) before we drove it away. Other avian predators are Lanner *(Falco biarmicus)* and Peregrine Falcons. We have recorded these falcons on the study area only a few times.

Disease apparently sometimes kills woodhoopoes. In late July 1977, a female that had nested unsuccessfully was conspicuously unwell; although she did not appear to be injured, she could fly only weakly and moved in a lethargic manner with drooping wings. She was gone when we returned to Kenya in late December of that year. Finally, the dried body of an adult male helper (about three years old) was found on the ground in its territory in January 1978. The body was completely intact and undamaged, suggesting that it had died of causes other than predation.

In short, apparently three major sources of mortality exist in woodhoopoes: nocturnal predation by arboreal mammals and driver ants, diurnal predation by birds of prey, and probably disease. The first of these appears to be by far the most significant.

Flock Size and Mortality

Beginning in January 1976 we censused flocks biannually and thus recorded probable mortality for each six-month interval. We found that deaths of woodhoopoes are independent of flock size. However, by contrasting the percentage of mortality per flock at six-month intervals, we find a highly significant ($P<0.01$) relationship for those flocks that suffered losses. This means, of course, that loss of one or two birds affects factors related to flock size, such as territorial defense, differently in small and large flocks. Moreover, small flocks are vulnerable to total extirpation. During this study, we recorded the disappearance of six groups, numbering from two to five when last censused. In contrast, no flock of six or more birds has disappeared altogether within a six-month period.

The Oil Gland as a Chemical Defense Mechanism

Dallas (1867, *in* Elder 1954) first suggested that the repellent secretion of the oil gland in Hoopoes might serve to protect incubating females and later their young. Later, Coupin (1914, *in* Elder 1954) and Ghindi (1906, *in* Elder 1954) claimed that Hoopoe nestlings store the secretion, discharging it in large amounts at potential predators. Austin and Singer (1961) state that woodhoopoes have a musky body odor during the breeding season similar to that of the Hoopoe, and Chapin (1939) commented that the disgusting odor of both adult and young woodhoopoes was like that of asafetida. We have handled and smelled well over 200 Green Woodhoopoes, and our observations may clarify some details concerning the oil gland and its function as a defense mechanism in this species.

Green Woodhoopoes have a well developed oil gland, naked except for a ring of small tuft-like feathers surrounding the opening at the tip of the papilla. The oil produced is clear and strongly odoriferous. Treating the feathers with this oil results in the characteristic odor of Green Woodhoopoes.

A possible function of the odor was made clear to us as we plugged roost cavities at night. We often looked into roosts with a flashlight, and sometimes were able to see the birds' responses to our intrusion. Disturbed woodhoopoes shuffled around in the hole, positioning themselves with their rear-ends facing the entrance. They elevated the feathers of the lower back, exposing the oil gland, and a large drop of oil rapidly formed on the tip, emitting a pungent odor. This physiological and behavioral response is present in both adults and feathered nestlings. It is not a breeding-season or nest-restricted phenomenon. Woodhoopoes responded similarly throughout the year when we peered into their roost cavities. The aromatic nature of the oil apparently is highly volatile. The odor emitted by frightened birds is sensed abruptly by the human observer, but its intensity quickly wanes, suggesting that the compound responsible for the smell breaks down in a short time. We have never seen large amounts of oil discharged, as has been suggested for *Upupa* nestlings. However, young woodhoopoes taken from the nest do release large amounts of malodorous, runny excrement. Perhaps a similar response actually occurs in *Upupa*.

The emission of oil in response to disturbance at the roost entrance strongly suggests nocturnal predation at roosts by mammals as a selective force favoring this unusual chemical defense mechanism. However, their chemical defense clearly is far from totally effective.

An alternative hypothesis regarding the function of "smell emission" in woodhoopoes is that the smell serves to defend their roost holes from acacia rats. These large (about 200 gm), nocturnal, arboreal rodents are abundant in cavities and crevices of large yellow-barked acacias, and they compete with woodhoopoes for cavities; acacia rats have taken over woodhoopoes' roosts on several occasions. Perhaps the odoriferous oil serves as a rat deterrent, preventing rats from entering the birds' roost cavities, at least while the woodhoopoes are present.

The volatile nature of the oil largely precludes a scent marking function. The odor seems not to linger for long periods; thus, it is unlikely that the odor is used to mark possession of holes.

The Annual Cycle

Seasonality

Although our study takes place near the equator, distinct seasonality occurs in most years as a result of the temporal distribution of rainfall. The major and most nearly consistent pattern is little rainfall from September or October into or through March of the following year. Conditions thus become progressively drier and possibly more stressful during this interval. Typically, the dry season is rather abruptly terminated in April, with the coming of the "long rains." The April rains appear to be the most distinctive and predictable climatic event of the annual cycle (Figure 6).

Rainfall and Breeding

Rainfall is the environmental factor that, more than any other, influences the onset of nesting of Green Woodhoopoes. We recorded no nesting starts on the study sites from December 1975 to April 1976. We located two nests in January 1977 on the south side of Lake Naivasha, but recorded no nesting activities on the main study area, Morendat Farm, at that time. In 1975, first broods fledged around 1 August, suggesting that breeding had begun somewhat synchronously around 1 June. Only one nest was present in the three study sites at the time of our first departure from Kenya in May 1976. When we returned at the end of 1976, several flocks contained independent juveniles of two broods, again suggesting that breeding had begun in June. Thus, although the rains were below normal in 1976, the woodhoopoes began nesting at about the same time as the previous year. In 1977 the April rains were extremely heavy (Figure 6), yet when we arrived on 2 June, nesting was under way in only one flock. However, within two weeks most flocks had eggs.

The uniform initiation of breeding (1975 to 1977) four to six weeks following the beginning of the long rains, despite great variation in total precipitation, suggests that the woodhoopoes respond to events triggered by the rains, such as the emergence of new vegetation and the corresponding increase in insect abundance, rather than to the quantity of moisture itself or other, more immediate effects of it. The most important ultimate factor, we feel, is the appearance in June and July of great numbers of larval lepidopterans and coleopterans. These larvae are extensively fed to incubating females and nestlings, making up a vast majority of the identified food items brought to nests in 1977.

Because we have no good evidence that food is severely limited for adult woodhoopoes at any time of year, and because insectivorous Palearctic migrants are abundant during the driest part of the annual cycle, we suggest that quality of food, rather than quantity, limits the breeding activities of these birds. That is, larval lepidopterans, in particular, appear to be requisites for successful rearing of nestlings. The time-energy relationships concerned with caring for young, such as trips to the nest with low quality items, may largely preclude effective breeding activities in the absence of plentiful larvae, or it may be that nestling woodhoopoes are physiologically specialized for use of larval insects.

Breeding

Mate Choice and Pair Bond

Because new flocks often form by the merging of groups of siblings of the same sex and because one member, the oldest of each group, is dominant to the others of its sex, the oldest male and female usually become the breeders. We have recorded this pattern in six groups of immigrant male woodhoopoes and in six groups of immigrating females as well.

In two cases a correlation between age and breeding status did not hold. In late May or early June 1977, three male siblings joined two females—a mother and daughter—in the females' territory. The dominant male (YL) apparently chose to mate with the younger female (YR) although both she and the older female (OR) exhibited prenesting sexual behavior. Both females entered the nest cavity for extended periods, often at the same time, to compete for food delivered by the males. The unresolved conflict between the two females for breeding status may have led to the destruction of the first clutch of eggs and desertion of the nest. With the onset of the second nesting, the dominant male repeatedly behaved aggressively toward the older female, vigorously supplanting her at the nest entrance by pecking her and grasping her wing or nape feathers in his bill and pulling the older female away. Thereafter, she ceased to compete with her daughter for breeding status and became an active helper.

In another newly formed flock, the oldest of three male immigrants also chose a daughter over her mother, as evidenced by courtship feeding, close escort of this female, and copulations. Here, however, the male did not become aggressive toward the old female. Apparently the mother's sexual behavior toward the younger males caused disunity in the flock that prevented her daughter from nesting from early June 1977 until our departure from Kenya in early August. This flock produced no young in 1977.

Certainty of Paternity

Paternity in birds is rarely known. However, in monogamous species, males exhibit behaviors designed to minimize the chances that they will be cuckolded. Typically these behaviors include closely guarding the female, especially before the eggs are laid. In Green Woodhoopoes where several adult males remain close to the breeding female prior to nesting, guarding behavior by the breeding and dominant male is pronounced. However, the overt aggression shown by the dominant male toward others varies from bird to bird. Some alpha males allow their brothers to feed the female as the flock moves through its territory, whereas others are physically aggressive toward other male flock members.

Behavioral interactions between the breeding male and his male flockmates become more pronounced at the termination of egg laying and the onset of incubation. Often the alpha male interferes with the interaction between his mate and another male simply by interposing himself between the two. Or, he may attack and peck at the other male. Following such aggression, the dominant male then "appeases" the other bird by grooming it or by initiating a vocal Rally. The adaptive significance of this seemingly ambivalent behavior is clear. The alpha male attempts to insure his paternity by keeping other males away from his mate during the likely period of egg fertilization. At the same time he must permit and encourage other males to bring food to the incubating female, and later to his offspring. This appears to be accomplished in some cases by permitting subordinate males of the flock to interact sexually with the female *after* the eggs are laid and incubation is well under way by "courtship" feeding, precopulatory behavior, and occasionally copulation. This, in turn, results in a large contribution of food to the female and young by the subordinate males. Perhaps such males are in effect deceived by the breeding pair in that they respond to the female and young as though they were the parent.

Unlike many birds, pairs of Green Woodhoopoes copulate conspicuously and comparatively frequently. The male initiates copulation, placing one foot on the back of the female and moving it back and forth in a scratching motion. The male then steps up on the female and moves the feet alternately up and down in a pedaling motion as the wings and tail of the female vibrate.

An unusual aspect of copulation is its duration. We have timed copulations that lasted as long as two and one-half minutes. The extended period apparently required for successful matings may be of adaptive significance in that "stolen" copulations resulting in insemination must be rare. That is, little likelihood exists that subordinate males will fertilize eggs because an

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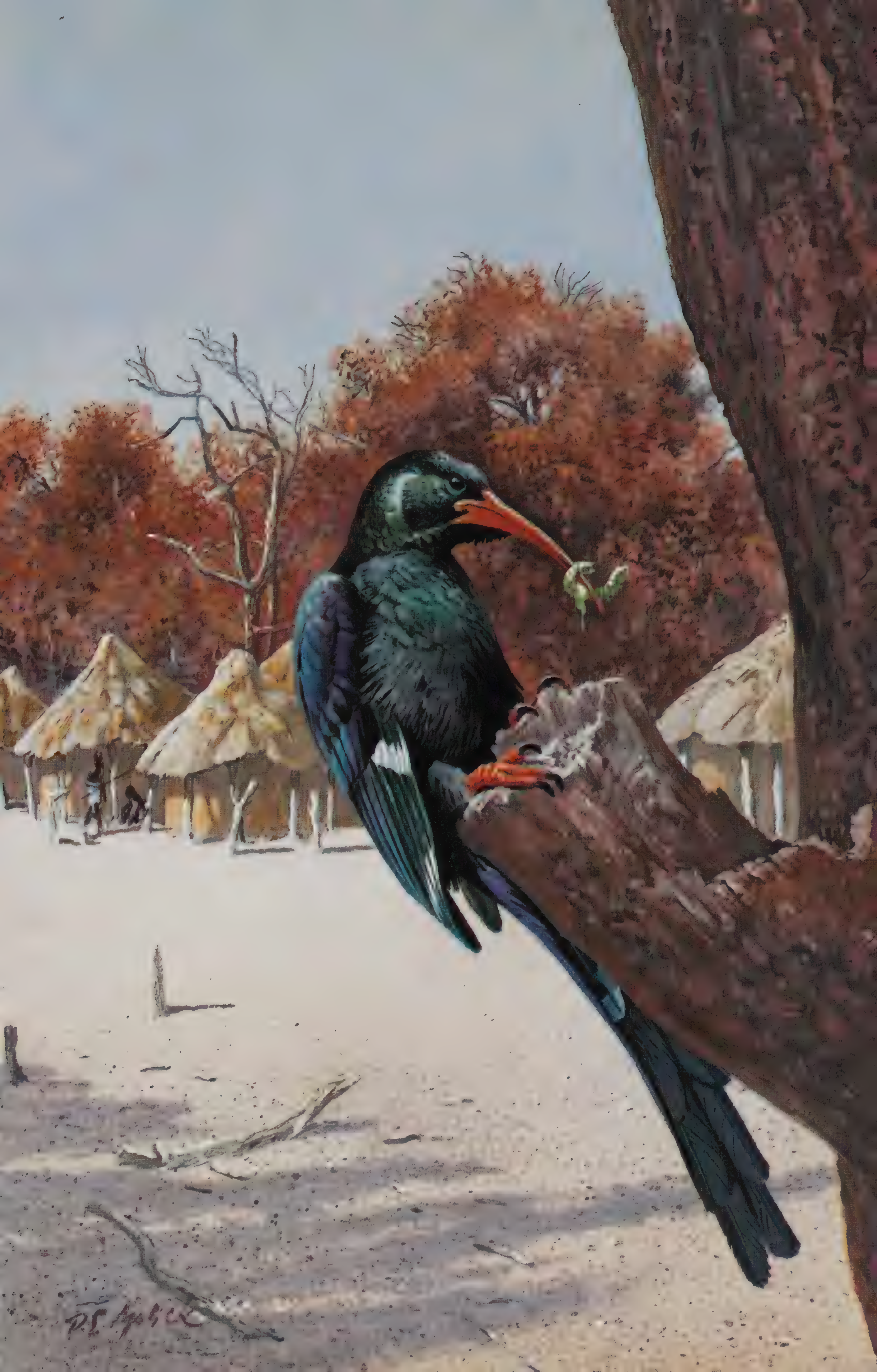
Green Woodhoopoe, *Phoeniculus purpureus*. Painting by Donald Leo Malick.



attempted copulation will be detected by the nearby alpha male before it can be completed.

Thus, confidence of paternity in Green Woodhoopoes probably is high, both because the alpha male assiduously guards his mate before the eggs are laid and because the prolonged duration of copulation makes a quick, "stolen" mating very unlikely.

Parentage

All offspring produced in a flock are those of the breeding pair, so long as both members remain alive. In 1975, egg predation occurred at two nests; both flocks contained other mature females, yet the original breeding bird laid a second clutch of eggs. In those flocks that nested twice (three times in one case), it was the same female who incubated and remained in the nest with the newly hatched young, with one exception. Here, the original breeding female apparently was taken by a predator in August; another female flock member (CGR) then nested. After the single young had hatched, a second female (CBR) then began to remain in the nest for extended periods, gave the twittering call as she solicited food from other flock members, and in general often behaved like the mother (see below). The juvenile disappeared at the time of fledging and a short time later the second female (CBR) laid eggs and began incubating. This nest soon failed, possibly because other flock members failed to provide adequate support for her. The first female (CGR) then bred successfully in 1976 and 1977. This situation, where two birds in the same flock and of the same sex attained breeding status while both were still alive, is extremely rare. (See the section on Mate Choice and Pair Bond for the two other exceptional situations.) All of our other evidence indicates that once a woodhoopoe attains breeding status, this position is retained for as long as the bird lives. All three exceptions are females who were chosen as a mate by the dominant male.

Nest Sites

In our study areas the Green Woodhoopoe usually nests in cavities in yellow-barked acacia trees, although two were in fence posts and one was on

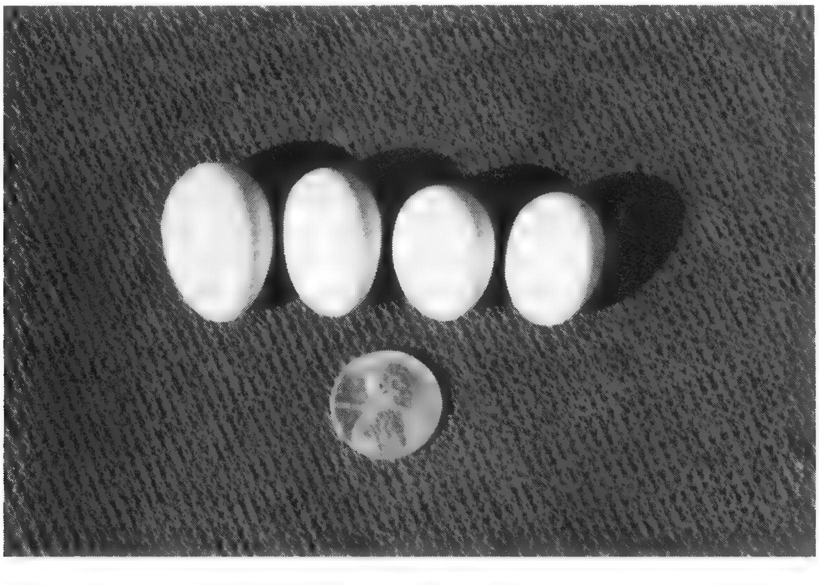


Figure 7. A clutch of four Green Woodhoopoe eggs; note the variation in size. Although all of these eggs contained embryos, only one hatched.

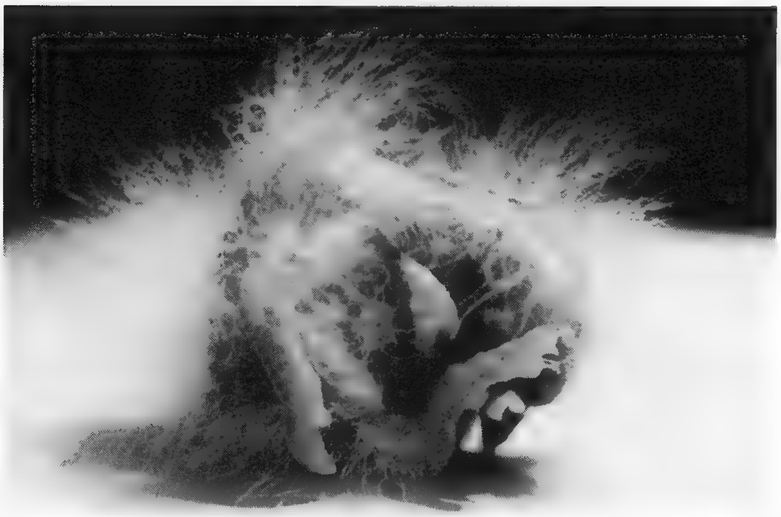


Figure 8. Close-up of a Green Woodhoopoe chick about 48 hours old, illustrating the woodpecker-like heel pads and protruding lower mandible.

bare ground underneath a piece of heavy farm machinery. The last three nests were those of the same female, indicating both scarcity of more suitable nest sites in her territory and the variation in nest site acceptability in woodhoopoes. Of 51 nests of marked flocks, 16 were in natural cavities in snags or knotholes and 34 were in old woodpecker excavations. Three kinds of woodpeckers, Nubian, Bearded, and Grey, occur on the study area, with the Grey Woodpecker being the smallest and most common. Cavities excavated by Grey Woodpeckers are most frequently used by the woodhoopoes, both because more of them exist and because holes of the two larger species are much in demand by other larger and more aggressive hole nesters such as Lilac-breasted Rollers and Blue-eared Glossy Starlings.

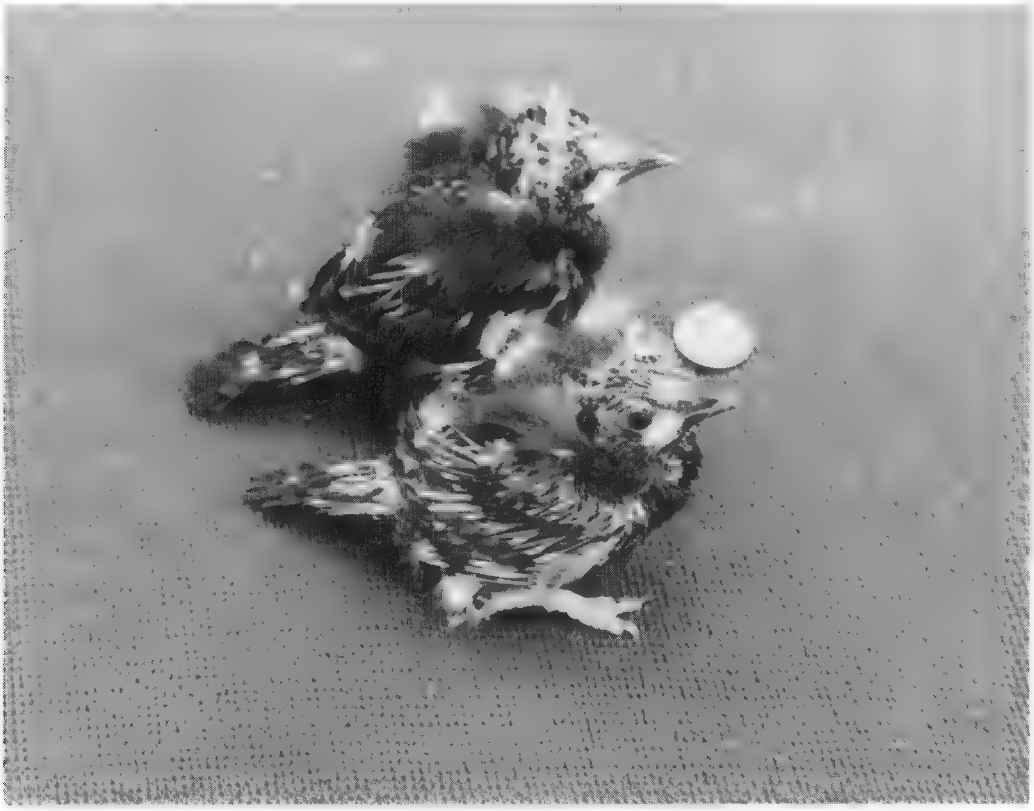


Figure 9. Two juvenile female Green Woodhoopoes at 16 days of age.

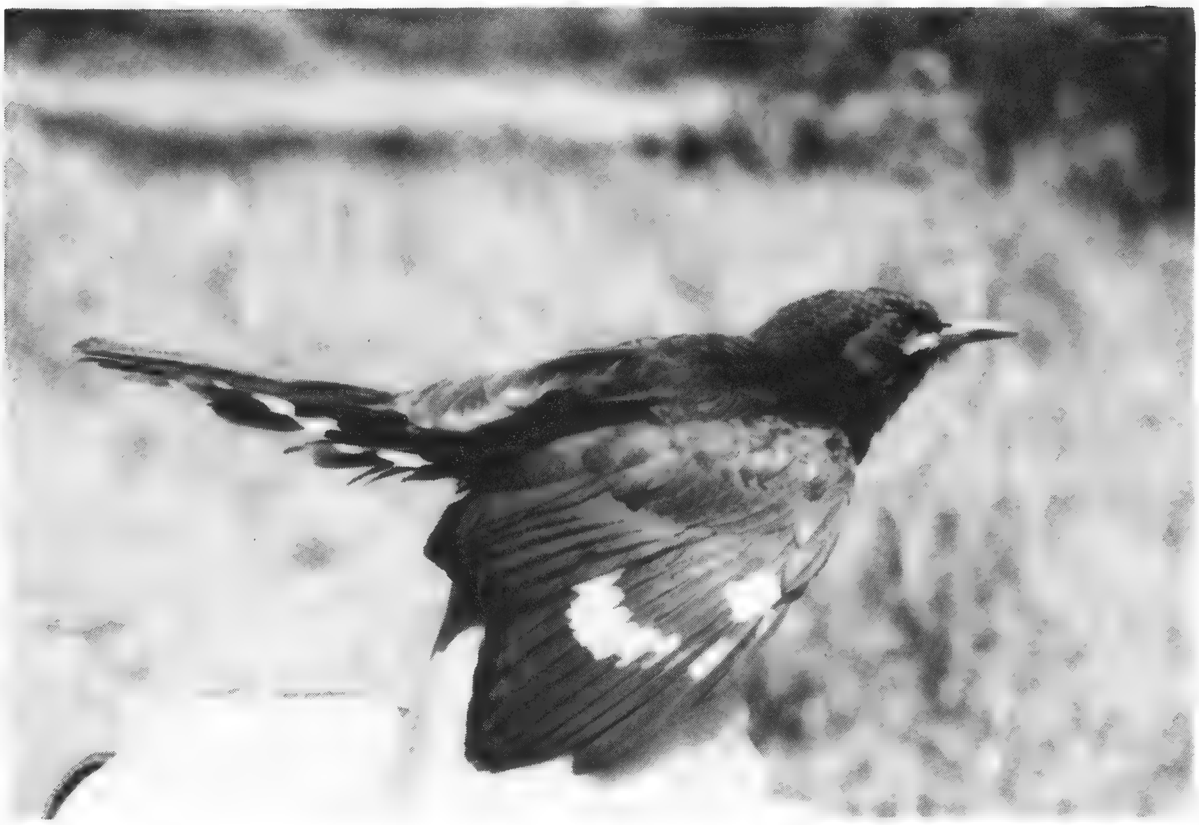


Figure 10. Juvenile female Green Woodhoopoe, 28 days old, just prior to fledging.

Woodhoopoes make no attempt to conceal the location of their nests, apparently relying altogether on its inaccessibility to predators. Before, during, and after egg-laying, most or all flock members frequently vocalize loudly at the nest. This behavior becomes more common when the nestlings are old enough to climb to the cavity entrance. The rarity of nest predation—no more than 24 percent of the nests we have studied—as compared to many other tropical, hole-nesting species (Skutch 1966) attests to the ability of these birds to choose secure sites.

The 50 nests placed above ground level ranged in height from 0.9 meters to about 22 meters. The flexibility shown by woodhoopoes in their choice of nest heights probably reflects both the scarcity of suitable sites and the intense interspecific competition for them.

No nest material is placed in the cavity and any grasses or feathers placed there by other birds are removed prior to nesting, often by several or all flock members. In contrast, the related Common Scimitar-bill *(Rhinopomastus cyanomelas)* places lichens and/or mosses in the cavity (pers. observ.).

Egg Laying, Clutch Size, and Incubation

We have relatively few data on egg laying, clutch size, and hatching success, partly because of the difficulty of looking into nest cavities. However, by use of a small mirror and flashlight, we obtained information on clutch size and hatching success for 16 nests. In these, the blue eggs numbered two to four (Figure 7); the mean clutch size was 3.19; and the mean number of young that hatched was 1.25.

Our data suggest that females lay eggs daily. The female parent only performs incubation, during which she is fed by her mate and other flock members. At one nest the incubation period was about 18 days and apparently began with either the last or penultimate egg. In this nest two young hatched at about the same time, 17 days after the clutch of four was completed, a third hatched a day later, and the fourth egg did not hatch. Incubation thus could have begun with the laying of the second egg, but because one egg did not hatch, we could not determine this.

Hatching Failure

At least one egg failed to hatch in nine of the ten nests where clutch size and number of eggs hatched were known. For these nests the mean number of eggs was 3.1 and the mean number of hatchlings was 2.0. In only one nest (four eggs) were all eggs known to hatch.

Numbers of young fledged in many other nests also suggest that young produced are fewer per nest than eggs laid. Although four eggs made up the clutch size in 44 percent of the nests for which this information is known, we recorded four fledglings only once out of 37 groups of fledglings. Evidence for partial brood reduction by starvation of nestlings is very rare. Although one young died in one nest, it seems unlikely that starvation was the cause, since 12 helpers brought food to the nest and the other three nestlings were of normal weight at fledging.

Because most flocks contained more than one female, one might suspect that unhatched eggs were produced by an individual other than the parent. Our behavioral observations suggest that this is unlikely. We rarely saw females other than the breeder enter a nest before the eggs hatched, and when this occurred, the visiting female remained only briefly (342 hours of concentrated watches at 22 nests during incubation). Moreover, one small flock contained only one female and only one of her three eggs hatched.

Thus, the apparent anomaly of an "extra" egg(s) that does not hatch appears to be the norm. We suggest that the unhatched egg or eggs is an adaptive but inefficient means of brood reduction. Both the colored eggs and use of nest material by some members of the family suggest that hole-nesting and absence of nest materials are recently developed characteristics of Green Woodhoopoes. We view the regularity of an unhatched egg as an adaptive response to environmental and societal selective pressures, going hand in hand with certain other K-selected traits, such as extended parental care and delayed breeding (Brown 1974).

Nestlings and Their Care

Green Woodhoopoes are altricial, as are other coraciiform birds. Newly hatched birds appear to be well covered with long white down, but after they are a few days old the downy covering appears sparse as a result of body growth without increase in plumage. Heel pads are well developed (Figure 8).

The female parent remains in the nest almost continuously from the time the young hatch until they are about two weeks old (Figure 9). The mother then spends an increasing amount of time outside the nest, often perched quietly in or near the nest tree. Because other flock members often pass food to the breeding female rather than directly to the young nestlings, and because the female parent often is unseen until she appears at the nest with food, it is difficult to assess accurately the foraging contribution made by the female parent. However, it surely is low at nests with helpers. The greatest percentage of feedings that we recorded by a female parent was 12 percent. This flock had three helpers.

TABLE 1

Feeding Contributions to Incubating Female

Flock	*Number of hours of observation*	*Total feedings**	*Percentage of feedings by male parent*	*Number of helpers*	*Percentage of feedings by helpers*
AD†	29.75	125	59	1	41
PF†	33.75	135	30	4	70
ST†	16.00	66	44	4	56
BF†	20.00	154	19	5	81
KG†	26.00	117	38	6	62
DD†	20.50	105	29	7	71
LH	17.00	56	80	3	20
AD	12.50	79	39	3	61
KG	25.50	109	70	3	30
H5	13.00	71	77	1	23
DD	15.50	93	53	2	47
ST	11.00	74	36	6	64
KK	7.00	84	20	4	80
BRF	14.50	90	47	3	53
MSG	7.00	39	56	4	44
PF	7.00	40	35	3	65
3-S	16.50	116	31	2	67
MT	13.00	59	34	3	66
Cr	8.25	52	35	6	65
Co-op	4.00	40	50	2	50
WF	17.00	151	25	6	75

*Only visits to nest with food are recorded.
†Nests observed in 1975. Others observed in 1977.

The nestling period is long, about 30 days, and the young are well developed before they fledge (Figure 10). As the nestlings mature, the male parent and other flock members feed the young directly most of the time, rather than passing food to the female parent. Often they actively avoid the female parent, who may attempt to take the food from the helpers. In addition to delivering food to the nestlings, helpers frequently preen and vocalize to the young birds. We have argued elsewhere that this behavior serves to promote personal bonds between nestlings and adult members of the flock, and that the nestlings themselves are potentially valuable resources to each older member of the group (Ligon, in press; Ligon and Ligon 1978).

The Role of Helpers

In some studies of communal breeders, all flock members are referred to as helpers, without consideration of the variation in contributions by individuals. It is now recognized that each individual in a social unit may follow methods of social interaction geared to its own personal benefit (Stallcup and Woolfenden 1978; Woolfenden and Fitzpatrick 1978).

In 1975 we had little knowledge of the kinship ties within the flocks we studied or the options available to birds of different age and sex categories. However, by June 1977 we had extensive knowledge of family relationships for a majority of our marked flocks and could begin to assess methods used by flock members that appear to aid nestlings and thus enhance the reproductive success of the breeding pair. These are: provisioning the incubating female and later the nestlings; "auntie" behavior; and putting to roost or "tucking-in" recently fledged juveniles. In addition, the roles of non-breeders in territorial defense, defense of the nest cavity, and mobbing of potential predators surely contribute to the welfare of the young.

Feeding the Incubating Female

During incubation nearly all of the nourishment of the breeding female is provided by her mate and other flock members. We watched 21 nests as the females incubated, and recorded food deliveries by each flock member (Table 1). Visits to the nest without food are not included in this analysis (see Stallcup and Woolfenden 1978). In most cases the contributions of helpers as a group were high; however, a great deal of variation in feeding rates was recorded between helpers within a given flock. This variation did not appear to be related to the number of helpers.

When flock members return to the nest area or tree, the incubating female solicits food by a distinctive vocalization—a rapid, continuous twittering (also see Rowan 1970). Sometimes the female pursues flock members, including her mate, while continuously emitting this call. This chasing and begging apparently is related to the female's degree of hunger; later it also reflects the hunger of small nestlings. When food has not been delivered to the incubating female for some time, she may leave the nest, locate the flock

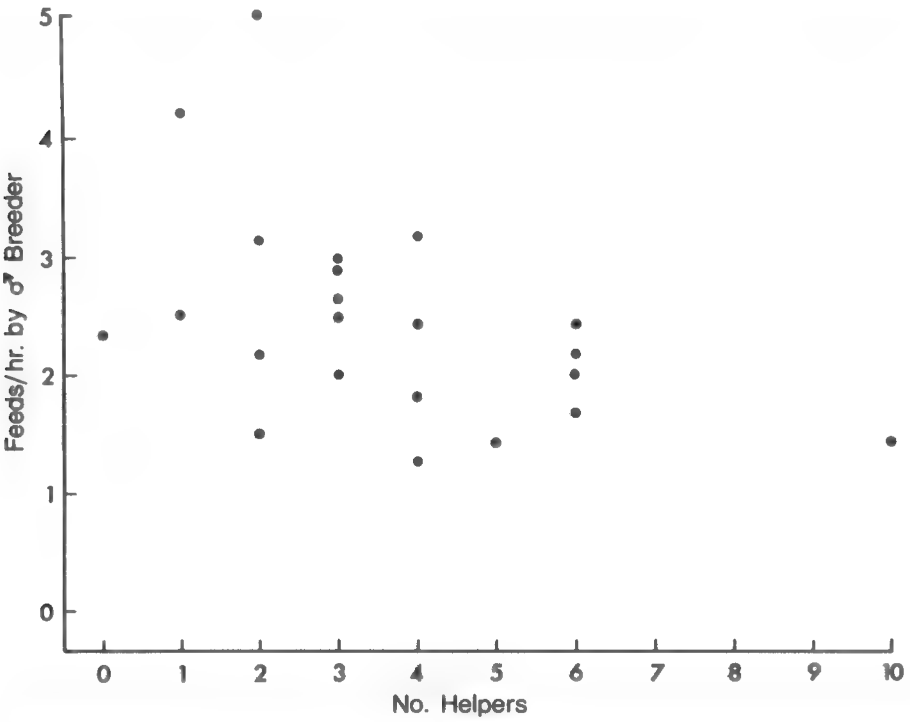


Figure 11. The inverse relationship between feedings of the incubating female by the male breeder and the number of helpers. $P<0.05$.

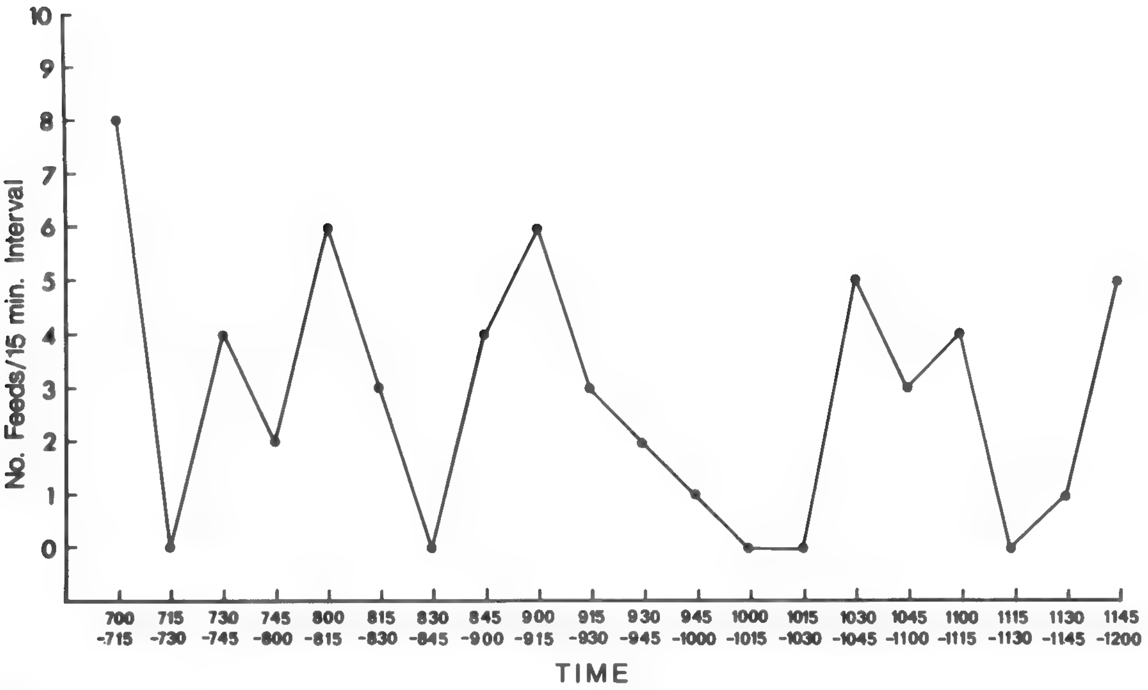


Figure 12. The temporal pattern of food delivery to the incubating female during part of an all-day watch at one nest.

by loud vocalizing and, after receiving a response, begin twittering intensively. This usually serves to bring the flock to the vicinity of the nest and to initiate a bout of provisioning by the flock members. Thus, the female parent controls to some extent the rate and periodicity of food delivery by other flock members to herself and later to small nestlings.

Nest helpers also reduce the feeding visits of the male parent to the incubating female. The inverse relationship between feedings by the male parent and number of helpers (Figure 11) is statistically significant ($t = -2.40$, $P<0.05$). The data are based entirely on deliveries of food to the nest; thus, they do not reflect the number of times the female was fed away from the nest, the size (quality) of the food items brought, or the extent to which the incubating female fed herself. These factors are more important in the small flocks, where females tend to leave the nest to forage and/or solicit food more frequently than do females in larger flocks. This also suggests a secondary advantage of helpers to the female breeder: the female may run less risk of predation by remaining at the nest.

The flock often returns to the vicinity of the nest together and engages in bouts of feeding the incubating female (Figure 12). This appears to be efficient in terms of time and energy expended. By returning to the nest area to forage for the incubating female, and later the nestlings, flock members decrease the time involved in delivering food; more trips to the nest with food can be made per unit time as a result of the short distances traversed. Moreover, each individual presumably is less vulnerable to predation by remaining within the group (Alexander 1974). Thus, travel to the nest with other birds, and foraging near it, should be less risky as a group activity.

Feeding the Nestlings

Helpers also make major contributions of food to nestlings, providing up to 83 percent of all feeding trips to the nest. The relationship between the number of helpers per flock and their feedings is shown in Figure 13.

Feedings of nestlings, like those of incubating females, are unevenly distributed through time. A portion of an all-day watch at one nest illustrates the temporal irregularity in delivery of food to the nests (Figure 12). The longest elapsed time between feedings was 52 minutes. As mentioned above, flocks tend to move through the territory together and to return together to the vicinity of the nest. Much of the food given to nestlings thus is gathered close to the nest. On one occasion we were able to observe the male parent continuously for 25 minutes as he foraged near the nest. During this time, he captured four very large grubs, three of which he took to the nestlings. Another male breeder captured four items from or below the nest tree in five minutes; all were fed to the young. These and numerous similar observations clearly suggest that the area near the nest is largely reserved for foraging for nestlings. Ricklefs (1971) describes a similar pattern for Mangrove Swallows *(Iridoprocne albilinea)* that were feeding nestlings. However, not all food taken to nestlings comes from near the nest. As the flock returns to the nest area, often from a long distance, many individuals may carry large food items for the young.

To sum up, nest helpers in the Green Woodhoopoe provide a large portion of the food brought to nestlings, serving to ease the burden of the parents. Rates of food delivery by male breeders vary widely from 1.31 per hour (four helpers) to 5.65 per hour (one regular helper). The number and age of nestlings, the number of helpers, and other factors must play roles in determining feeding patterns by male parents and by individual helpers.

Recently, Stallcup and Woolfenden (1978) have shown that male helpers in the Florida Scrub Jay make more feeding visits to the nest than do female helpers. This difference is attributed to the possibility that male helpers gain breeding status by the addition of flock members, whereas females do not (Woolfenden and Fitzpatrick 1978). In woodhoopoes, because either sex may inherit the territory or move with siblings to an adjacent one, a mature helper of either sex probably gains by the addition of younger flock-mates—especially those of the same sex as the helper—and in 1975 female and male helpers contributed about equally to the welfare of nestlings (Table 2). Although this analysis obscures individual strategies, these data do illustrate

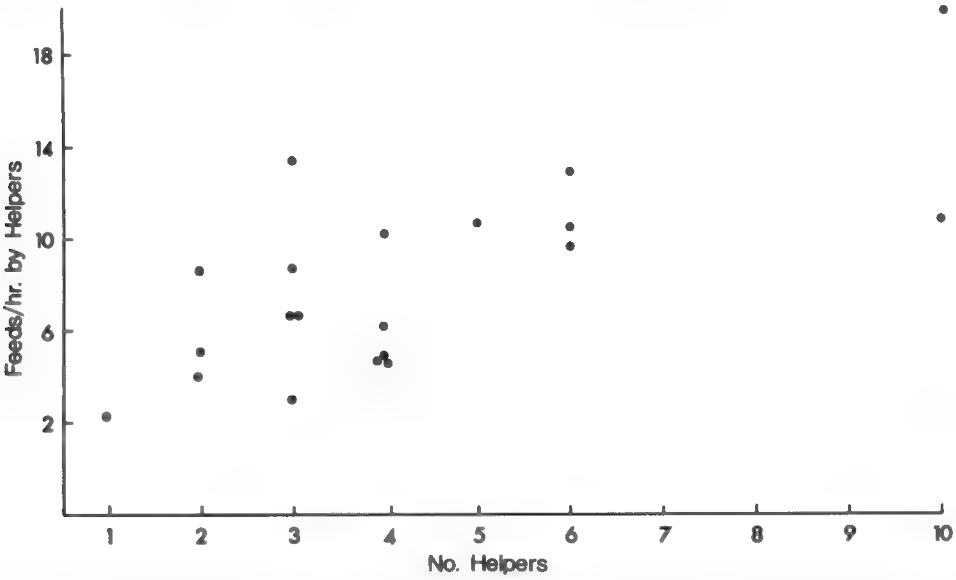


Figure 13. The relationship between feeding visits per hour by helpers and the number of helpers. $P<0.05$.

that in Green Woodhoopoes the sexes do not differ in any consistent way in their roles as helpers.

Auntie Behavior

We refer to unusually solicitous behavior directed to nestlings by non-breeding females as "auntie behavior." This does not necessarily infer either especially high feeding rates or a particular kinship tie. Rather, "aunties" appear to be most interested in personal contact with the young in the nest. In general, they act as surrogate mothers.

During incubation, future aunties generally feed the female parent as regularly as other flock members do. Female-female competition between the breeding female and the auntie for breeding status is non-existent here. Instead, auntie behavior is initiated after the young have hatched. At that time, other flock members pass food to the begging female parent in or outside the nest, who then delivers it to the young. Aunties prefer to feed directly, actively avoiding the twittering mother and entering the nest. An auntie also may enter the nest without food, often remaining several (two to ten) minutes. While inside the nest, she may assume the maternal role, twittering and begging for food from other flock members. When fed, the auntie transfers the food to the nestlings. In some flocks aunties also spend considerable time in the nest when the mother is present.

Often, aunties sit quietly at the nest, or in the nest tree, while the rest of the flock forages elsewhere. The female parent may or may not be in the nest at this time. This quiet surveillance may function to guard the cavity. Aunties defended the nest from Blue-eared Glossy and Superb Starlings and Grey Woodpeckers by aggressive swaggering and flights at the intruders, often

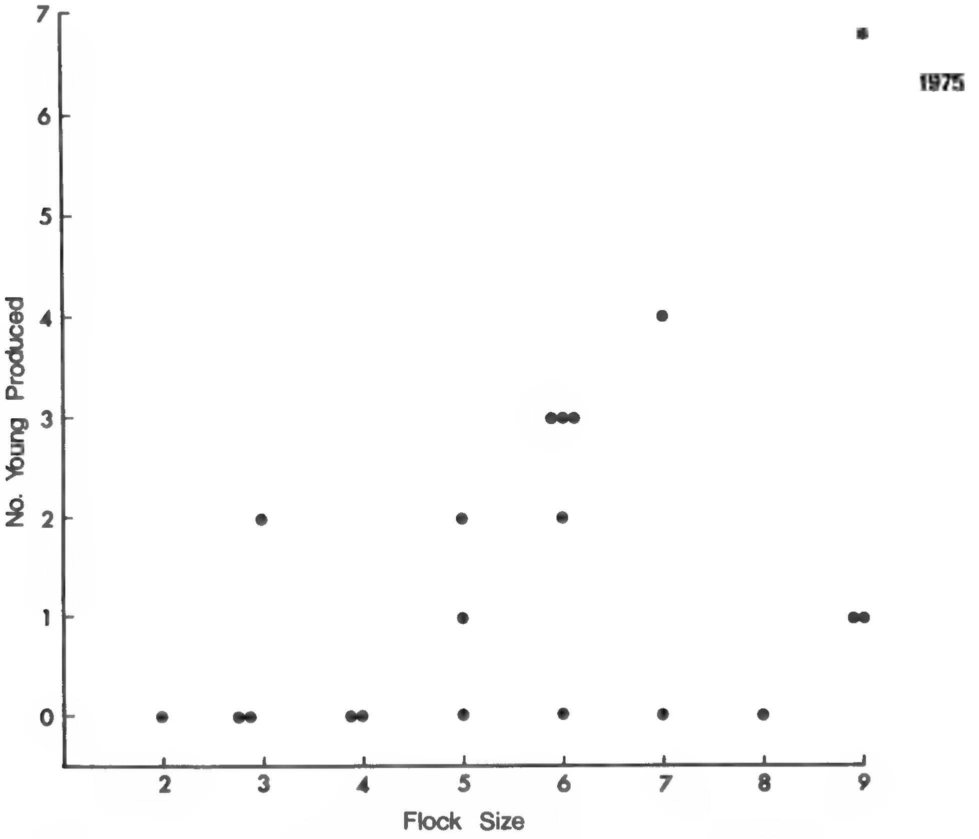


Figure 14. The relationship between flock size and the number of independent young produced in 1975.

TABLE 2

Feeding Visits by Helpers, According to Sex

Flock	*Number of hours of observation*	*Feedings per female helper per hour*		*Feedings per male helper per hour*	
DD-1					
I†	20.5	0.41	(3)‡	0.49	(5)
N§	32.0	1.00	(3)	1.10	(5)
DD-2					
I	—	—		—	
N	32.0	2.00	(4)	1.45	(6)
KG					
I	26.0	0.70	(2)	0.38	(4)
N	36.0	2.80	(2)	1.10	(4)
Cr					
N	31.0	0.93	(3)	1.94	(2)
ST					
I	16.0	0.65	(2)	0.50	(2)
N	25.0	1.20	(2)	1.20	(2)
B-1					
I	20.0	1.20	(4)	1.55	(1)
WWH					
I	14.0	1.20	(1)	1.30	(3)
RF					
N	31.0	0.85	(2)	1.33	(3)
$\bar{x}$		1.18	(2.55)	1.12	(3.36)

*Only visitations with food are included.
†Incubation.
‡Number of helpers.
§Nestlings.

supplanting them. When a group of four Superb Starlings landed on a nest snag, the auntie immediately entered the hole, turned around facing outwards, and blocked the entrance with her head and shoulders while jabbing at the starlings with her bill. One auntie was on guard and the female parent was in the nest when two Grey Hornbills *(Tockus nasutus)* came to the nest; both female woodhoopoes made repeated attempts to drive them away.

When the young are old enough to perch at the cavity entrance, they are groomed by all flock members, but here again aunties are especially attentive. Flock members direct vocal rallies into the faces of well grown young. Aunties vocalize to youngsters repeatedly, especially preceding or following a grooming session. This probably serves to “imprint” the young on fellow flock members.

Aunties certainly gain experience in parental behavior. They may also gain in that the nestlings may become closely attached to them. At most nests, aunties are not thwarted by the female parent; here aunties probably are daughters of the breeders, as is known to be true in some cases. However, at two nests where would-be aunties were unrelated to the nestlings, they occasionally were obstructed or mildly threatened by the female parent.

Tucking-in

All flock members continue to care for young woodhoopoes after they fledge. In addition to feeding and protecting them from predators, most flock members engage in a behavior that serves to guide the callow juveniles to roosting sites and to entice them to remain there; we refer to this as "tucking-in." Perhaps the most interesting aspect of this behavior is that it is a concerted group effort. We have seen up to nine individuals simultaneously directing youngsters to a roost hole. This action is repeated every night until fledglings have been out of the nest for about two weeks. About an hour before dark, all flock members except the young fly as a group to a tree, where they bunch up and direct rally calls toward the young. They then remain in that tree, giving excited single calls, until the fledglings fly to them. The adults fly again, working their way toward the roost tree, landing occasionally to rally. The young follow, gradually being led to roost. Young birds may be reluctant to fly at all, or at best may fly clumsily in the wrong direction.

In one case one of the two fledglings was fairly well coordinated physically, and successfully followed the rallies of the four adults. The other, however, was reluctant to fly; it had, perhaps, fledged on that very day. As three adults led the precocious youngster to the roost tree, the male parent remained behind with the slow fledgling. The male called repeatedly, flew to the juvenile and rallied, then flew to a nearby tree and called again. The young bird finally flew, but headed in the wrong direction. The male quickly flew in front of the flying fledgling and began gliding, exposing the white wing patches. The young bird corrected its flight path.

When fledglings finally arrive at their roost tree, much excitement occurs among the flock members. Several group rallies take place, and the young are led to the hole. An adult usually enters first. As soon as the young follow, a feeding bout begins. Adults bring in food, uttering low growls as they pass it to the begging juveniles in the hole. The whole process may last for up to 30 minutes. It is usually complete well before dark, and adults often resume foraging or quietly preen for some time before they go to their roosts. Even when adults share a cavity with fledglings, they usually enter the hole some time after the young are in. The same roost holes are not necessarily used every night for juveniles. Commonly, they alternate in the use of two or three roost sites from night to night.

The Relationship of Helpers to Reproductive Success

The effect of helpers on the reproductive success of breeders is one of the critical questions pertaining to the adaptive significance of communal systems. In several species, but not all, pairs with helpers rear more young than do pairs without helpers, or with fewer helpers (Emlen 1978). We hold the view that natural selection favors retention of helpers in the territory of the breeding (and dominant) pair only if it leads to a net increment in the breeders' reproductive success (cf. Zahavi 1974). However, it does not follow that more young per nest, or per year, must be produced by pairs with more helpers than by those with fewer for this requirement to be met. By retaining their offspring as helpers until a breeding site becomes available, the breeders may gain more than if they were to drive their grown young from the territory, even if these birds depress subsequent reproductive success of the parents. This is true because mature young are more valuable to the parents than eggs or nestlings (Fisher 1958). Moreover, we assume (like Stallcup and Woolfenden 1978) that helpers usually leave the parental territory when it becomes to their advantage to do so. We have observed woodhoopoes leave their territory on several occasions, with no hint of aggression on the part of the breeding pair. Sometimes a bird returns periodically to the territory that it had left earlier, further suggesting that departure is voluntary and is not initiated by aggressive interactions.

Thus, our premises are that parents gain by the presence of helpers and that helpers also benefit by remaining in an established territory and by providing aid to younger birds, although the ways in which they gain may be obscure. Gains to helpers could be via the genes shared with the recipients of aid (Brown 1974, Hamilton 1964); or they could derive more direct benefits, such as occupancy of a safe roost or experience in caring for young, or by later use of the younger birds to attain breeding status (see Woolfenden and Fitzpatrick 1978). The unisexual emigrations in woodhoopoes of groups composed of siblings of different ages support this last suggestion (Ligon, in press; Ligon and Ligon 1978).

To assess the overall effect of helpers clearly is difficult, and it cannot be accomplished within a short period of time (see Emlen 1978). Thus, our conclusions are to be taken as tentative. The year-to-year variation in the reproductive success-helpers analysis will in itself emphasize caution in evaluating the long-term effects of helpers.

The influence of helpers on reproductive success can be viewed in several ways: (1) flock size and number of young fledged per nest, (2) flock size and number of young attaining independence per annual cycle, and (3) reproductive output per flock over longer time periods, irrespective of changes in flock size. This last analysis might suggest that factors other than the number of nest helpers, such as territory quality, exert an important influence on reproductive output (Brown 1974).

Our data from 1975 permit the first and second kinds of analyses. For 1976 and 1977 we obtained information only on the number of young surviving to independence. Thus, for a three-year period we can evaluate reproductive success per flock, based on this criterion.

Flock Size and Number of Young Fledged per Nest

The relationship between flock size and number of young fledged per nesting attempt is not significant. Because we have only two observations suggesting brood reduction by starvation of nestlings (through 1978), regardless of brood or flock size, it is perhaps not surprising that helpers do not appear to influence directly the number of young woodhoopoes fledging per nest. Some other students of communal breeders likewise have failed to show a positive relationship between the number of young reared per nest and the number of helpers (e.g., the Striated Jungle-babbler, *Turdoides striatus*, Gaston and Perrins 1975; Gray-crowned Babbler, *Pomatostomus temporalis*, J. L. Brown, pers. commun.). These systems differ somewhat from those where helpers *vs.* no helpers comparisons are made. In many species, reproductive success per breeding effort is greater for groups than for pairs (Emlen 1978).

Flock Size and Number of Surviving Young per Year

Of more significance than the number of young fledged per nest is the number of surviving young produced during the annual cycle. Here, our measure of reproductive success is the number of young woodhoopoes surviving per calendar year to the following January. January is a good time to tally the previous year's production because, with very few exceptions, breeding activities have ceased and will not be resumed until the following June. We have looked at production of young from flocks of differing sizes in two ways. First, we tested for significant regressions of independent juveniles on flock sizes for each year. Second, we arbitrarily divided our marked flocks into small (two to five birds) or large (six or more birds) groups and compared the mean number of young surviving through January in the different flocks. Flocks that disappeared altogether during a year were excluded from these analyses. Because year-to-year variation was great, the results for each year are presented separately.

In 1975 we found a positive regression between the number of surviving young and the number of helpers (Figure 14). This regression is significant only if we omit from treatment those flocks in which the breeding female died, or nests that failed for reasons thought to be unrelated to flock size—predation, death of young by mites, and apparent desertion of the nest when an egg hatched. The other important factor influencing the regression is the large number of juveniles produced by Flock DD, which contained nine adults in late July 1975, plus three newly fledged young. The breeding female nested successfully again in September, and a third time in late November. This is the only flock for which we have any evidence of three successful nestings in a single reproductive period. Reasons for the third breeding effort are not known, but may be related to the territory quality, especially size, or to the number and quality of helpers. All nine mature birds, plus the three juveniles that fledged in July, actively fed the nestlings in January. In any case, the significance of the regression is based on eliminating certain failed nests from consideration, and on the extraordinary occurrence of three successful nestings in one flock.

The following year, 1976, the relationship between group size and the number of young attaining independence was positive, but not significant (Figure 15). Because we were absent during the nesting period, we included all marked flocks. In January 1977 on the south side of Lake Naivasha, we found females incubating in two adjacent territories. No breeding activity was recorded for any of 21 other marked flocks. The young produced were recorded in June 1977. Because these nests appeared to be part of the 1976 breeding cycle, they are included in the analysis for that year. Four young fledged from one of these nests, our only instance of more than three juveniles per nest, regardless of flock size.

Between January and June 1977 many breeders disappeared; thus, several social units were reorganized and reconstituted. Most of the marked flocks were small, five birds or less. In this particular year, small groups, including our only record of successful breeding by a single pair, fared better than did the few larger flocks of more than five birds (Figure 16). Especially noteworthy was the production of six young by a group of five, and five young by a group of three (two males and a female).

Comparison of reproductive success of small versus large flocks in each of three years also illustrates considerable year to year variation. In two of

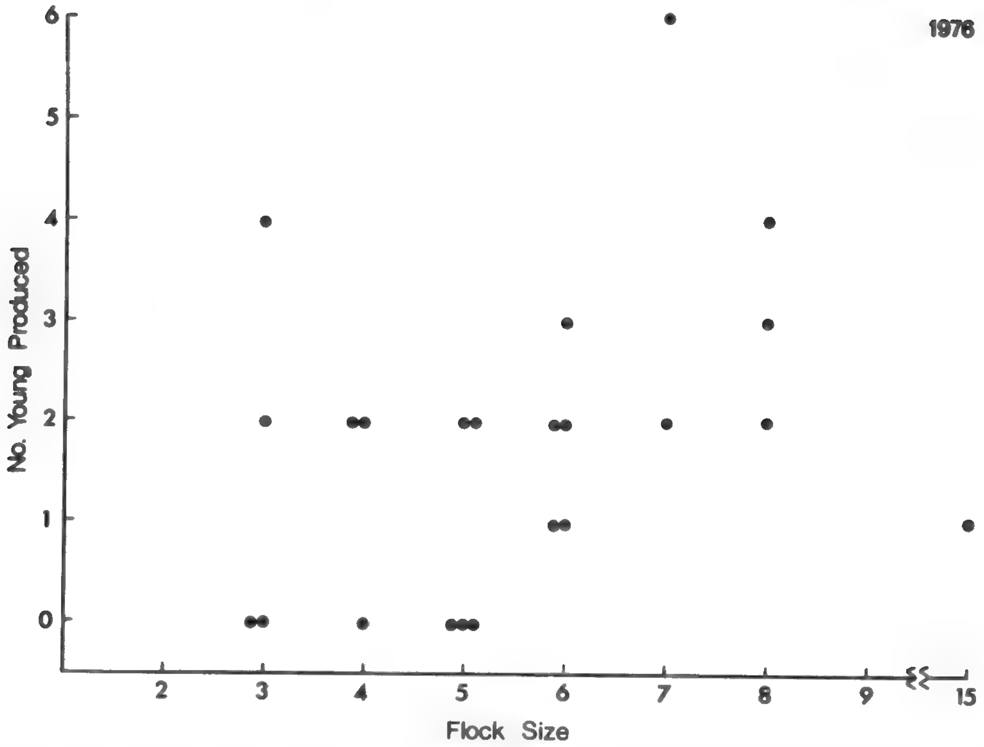


Figure 15. The relationship between flock size and the number of independent young produced in 1976.

three years, larger flocks surpassed smaller flocks in production of young woodhoopoes on a per flock basis (Table 3). However, also in two of three years, smaller flocks did better as measured by young produced per flock member.

These data do not clearly resolve for this species the fundamental question raised by Brown (1978), Emlen (1978), and Zahavi (1974): Do helpers assist in the raising of young or, in the case of woodhoopoes, are more helpers of greater help than fewer helpers? And, who is helped? Our data suggest that, more often than not, reproduction of the breeding pair is enhanced by the presence of four or more helpers, as compared with those pairs with fewer helpers. On the other hand, in two of the three years, the increment of young per flock member was greater for birds in the smaller flocks. For the three years combined, breeders and helpers in larger flocks did somewhat better than their counterparts in the smaller social units.

These kinds of gross comparisons of reproduction in large and small flocks possibly are somewhat misleading in that one may conclude that nest helpers increase reproductive success per year. However, it is likely that other factors, especially predation, have a greater effect on annual changes in flock size, including recruitment of juveniles, than the efforts of helpers. To the extent that larger flocks produce more young per year, this may in part be caused by secure nest and roost sites in those territories; that is, reduced mortality may be more important than producing young woodhoopoes. Thus, nest helpers *per se* may not explain most of the increased reproductive success enjoyed by breeders in the larger social units.

Reproductive Success per Flock Over a Three-year Period

Brown (1974) predicted that reproductive success in flocks of communal breeders should be similar from year to year relative to other flocks. He based this view on the assumption that territory quality controls reproductive success and that flocks in high quality territories should perhaps be larger and produce more surviving young than those flocks in territories of lesser quality. Our information on year-to-year patterns of reproduction per flock do not accord with these predictions (Table 4). For example, one small flock (AD) in 1975 suffered high mortality; two of the original three birds died and produced no young. Subsequently, this group became highly successful in terms of numbers of surviving young and total flock size. Another flock (DD), conspicuously successful in 1975, has been only moderately successful since that time.

Several factors must be considered in any effort to interpret year-to-year intraflock variation in breeding success. For example, death of a breeder can cause the breakup of a flock, or, if helpers are offspring of the breeding pair and males and females are represented about equally, reproduction in the flock can stop for an extended period, until most members of one sex or the other emigrate or die.

Overall, the most important measure of success by breeding woodhoopoes is the successful placement of their offspring in breeding positions, that is, as the dominant bird in an established territory. Between mid-1975 and January 1978 only eight marked flocks have produced any emigrants. Of the 14 emigrants attaining breeding status, half have come from only two flocks (DD and MSG); six of these are probably young of the two original breeding pairs. Two of the other seven represent breeders whose mates had died (one male, one female). The important point is that procurement by a young woodhoopoe of space for breeding is extremely difficult and the best parental strategy in this regard apparently is to permit young to remain in the parental territory until they can move in unisexual groups of two or more when a vacancy in another territory appears. Again,

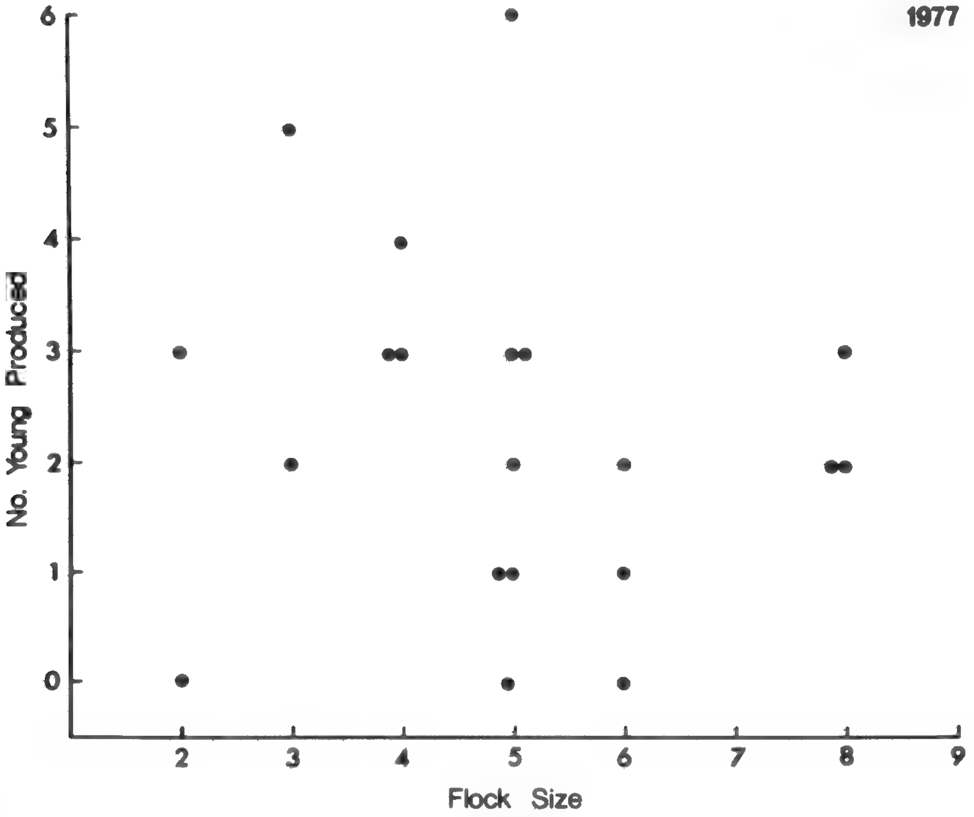


Figure 16. The relationship between flock size and the number of independent young produced in 1977.

TABLE 3

Mean Number of Juvenile Green Woodhoopoes Surviving to Independence in Small (2–5) and Large (>5) Flocks

	1975	*1976*	*1977*
Small flocks	0.35	1.33	2.40
Number of flocks	14	14	15
Juveniles produced per adult flock member	0.10	0.31	0.54
Large flocks	2.5	1.78	1.86
Number of flocks	10	9	7
Juveniles produced per adult flock member	0.33	0.23	0.31

Three Years Combined

Small flocks	1.29 juveniles per flock	0.32 juveniles per adult
Large flocks	2.00 juveniles per flock	0.48 juveniles per adult

TABLE 4

Rank Order in Production of Young per Year, by Territory

Territory	*Rank*		
	1975	*1976*	*1977*
DD	1 (7)*	16 (0)	4 (3)
KG	2 (4)	13 (1)	4 (3)
Cr	9 (1)	2 (4)	4 (3)
SS	3 (3)	16 (0)	18 (0)
ST	6 (2)	6 (2)	11 (2)
B	10 (0)	13 (1)	2 (5)
WWH	10 (0)	6 (2)	11 (2)
WF	3 (3)	1 (6)	11 (2)
PF	10 (0)	6 (2)	18 (0)
H-5	10 (0)	6 (2)	11 (2)
MSG	6 (2)	4 (3)	11 (2)
Co-op	6 (2)	16 (0)	4 (3)
LH	10 (0)	16 (0)	17 (1)
3-S	10 (0)	6 (2)	3 (4)
KK	3 (3)	4 (3)	4 (3)
AD	10 (0)	2 (4)	1 (6)
RF-1	10 (0)	16 (0)	4 (3)
RF-2	9 (1)	13 (1)	18 (0)
MS-4	10 (0)	6 (2)	11 (2)
MT	—	6 (2)	4 (3)

*Numbers in parentheses indicate number of young surviving to independence.

from both the parents' and helpers' viewpoints, emigration of two or more offspring when space becomes available is a sound strategy, simply because mortality is so high. The same argument holds for younger, subordinate birds emigrating with an older, dominant sibling. The younger bird might well attain breeding status as a result of the death of its older sibling. In fact, in nine cases of emigration by unisexual groups of certain or possible siblings, or when two birds of the same sex were initially found in a small flock, the older bird died before a younger one on seven occasions, with the result that the younger bird became the breeder.

To summarize, breeding pairs of Green Woodhoopoes attempt to maximize their reproductive output by producing two broods of young during the latter half of the calendar year. The fact that brood sizes tend to be small (one to three) regardless of the number of helpers suggests that two small broods of different ages yield more surviving young than one or more larger broods. Breeders may retain offspring of both sexes within their territory for several years, until the young birds have certain entry into a new territory. Moreover, by producing small numbers of young per brood, age staggering is increased and, perhaps as a result, a smooth dominance hierarchy develops with little overt aggression. This leads, in turn, to a high degree of apparent cooperation between unisexual groups of siblings when they emigrate to a new territory. However, as we have attempted to show, this does not mean that an individual emigrant is sacrificing any of its own reproductive potential for a relative; rather, given its position in the dominance hierarchy of helpers, and the high and unpredictable pattern of mortality, it appears that subordinates escorting a dominant sibling to a new territory ultimately have at least as good a chance to breed successfully as does the oldest, dominant bird.

Summary

Green Woodhoopoes *(Phoeniculus purpureus)* belong to the coraciiform family Phoeniculidae, a group restricted to the Ethiopian zoogeographic region.

In this paper we describe various facets of the biology of this communal species near Lake Naivasha, Kenya, where woodhoopoes are common in open stands of yellow-barked acacias *(Acacia xanthophloea)*. Our study began in July 1975. By May 1976 we had captured and marked 148 woodhoopoes for individual recognition. Subsequently, through January 1978, we have marked a total of 235 woodhoopoes in 28 flocks.

Social units or flocks of Green Woodhoopoes range from a pair to sixteen, with 92 percent of the groups studied numbering from three to nine. The sex ratio is usually balanced, although it may be strongly skewed one way or the other in any particular flock. Unlike many other communal species, sexual dimorphism in size and behavior is conspicuous, with males averaging about 20 percent heavier than females. All vocalizations of adults are sexually diagnostic. Bills of juveniles are black and gradually become red over a period of 12 or more months.

One of the most striking aspects of woodhoopoe behavior is movement to a new territory by unisexual groups of two to four non-breeders. Often such emigrants are siblings. This pattern of movement occurs only when a breeding vacancy opens up, or when a territory is weakly defended. Some females also exhibit this emigration pattern, but others, unlike males, disperse, either singly or in small groups. These females apparently wander

until they discover a territorial vacancy or until they encounter a male or males with whom they attempt to establish a new territory. Virtually all suitable habitat is owned by one woodhoopoe group or another, thus establishment of new territories occurs rarely. When such attempts are made, unrelated birds of the same sex may merge to form a new social group. This appears to be adaptive in that numerical strength is required to defend and hold space. The older, dominant birds gain both breeding space and the younger birds as helpers, while the younger "recruited" individuals gain territorial space and the advantages associated with dependable occupancy of a particular area. Moreover, if the older birds die, the younger individuals may "inherit" the territory, breeding status, and any still younger birds as their helpers.

Only one breeding pair of woodhoopoes exists in any flock, regardless of its size. In a flock in which the pair has remained intact for an extended period, and where breeding has occurred several times, most non-breeders are the offspring of the breeding pair. However, because of the unisexual emigration of siblings and because unrelated birds of the same sex sometimes merge, especially in small, decimated or newly-forming flocks, variance in relatedness in a given flock may be high. Most flock members at any time are related to one or both of the breeders.

We briefly describe various aspects of the general behavior of woodhoopoes: foraging, dominance and aggression within flocks, allopreening, vocal Rallies, territoriality, and Flag-waving. The Rally is an intraflock vocal display that apparently serves to promote flock unity. Flag-waving seems to incite other flock members and to coordinate territorial defense. The flag-waver carries a small, non-food item, such as a clump of lichens, to the scene of a prospective territorial fight, waves the item back and forth, and often extends it toward the opposing flock. The "flag" may also be passed back and forth between several flock-mates as the group intensifies its responses to the intruders.

Roost sites appear to be a critical limiting resource for Green Woodhoopoes largely because of the number of competitors for them. Although most potential competitors are birds, the acacia rat *(Thallomys paedulcus)* and honey bees *(Apis mellifera)* frequently pose severe problems for woodhoopoes in this regard. Mortality is high and appears most often to take place at the roosts, as a result of nocturnal predators. Both mammalian and insect (driver ants) predators are thought to be important. Green Woodhoopoes, like their relative the Hoopoe *(Upupa epops)*, emit a strongly odiferous substance from the oil gland when they are frightened. If this represents a chemical defense mechanism, as appears likely, it is not clear against what predators it is effective.

Breeding begins in June, apparently in response to the appearance in large numbers of larval lepidopterans. Our evidence indicates that larval lepidopterans are essential for successful nesting and that availability of this resource largely determines overall reproductive success in any given year.

The male and female breeder are almost always the oldest and dominant birds of their respective sex. Prior to the beginning of incubation the male breeder assiduously guards his mate from copulation with other males.

Most (34 of 51) nests are in old woodpecker cavities, one to twenty-two meters above the ground. No nest material is gathered, and any grasses or feathers placed in the holes by other species are removed. Clutch size ranges from two to four and the incubation period is about 18 days. Only the female parent incubates. At most nests at least one egg failed to hatch. The altricial young are brooded almost continuously by the female parent for the first two weeks of their lives. During this period other flock members deliver food to the mother, who eats it or transfers it to the nestlings. As the young develop, the helpers display a strong inclination to personally feed the nestlings, to groom them, and vocalize to them.

A significant inverse relationship exists between provisioning efforts of the male parent and the number of helpers; that is, helpers reduce the efforts of the male parent. After hatching, helpers as a group may make up to 83 percent of all feeding trips to the nest. A significant positive relationship exists between total feeding contributions by helpers and number of helpers. However, there is no significant relationship between flock size and the number of young fledged per nest. Nor is there a consistent relationship between flock size and the number of surviving young produced per year. Flocks with more than five birds produced an average of 2.0 juveniles per flock over three years, whereas smaller flocks produced an average of 1.3 young per flock. In two of three years, the larger groups produced more young per flock, while in two of the same three years, smaller units produced more surviving young per flock member. Differential mortality between flocks appears to be of greater significance than differential natality, in terms of over-all "flock success." Finally, our data suggest that most flocks occupying particular territories do not regularly do better or worse in terms of reproductive output than do other flocks. In short, possible differences in territory quality do not lead to predictable patterns of reproductive success.

Acknowledgments

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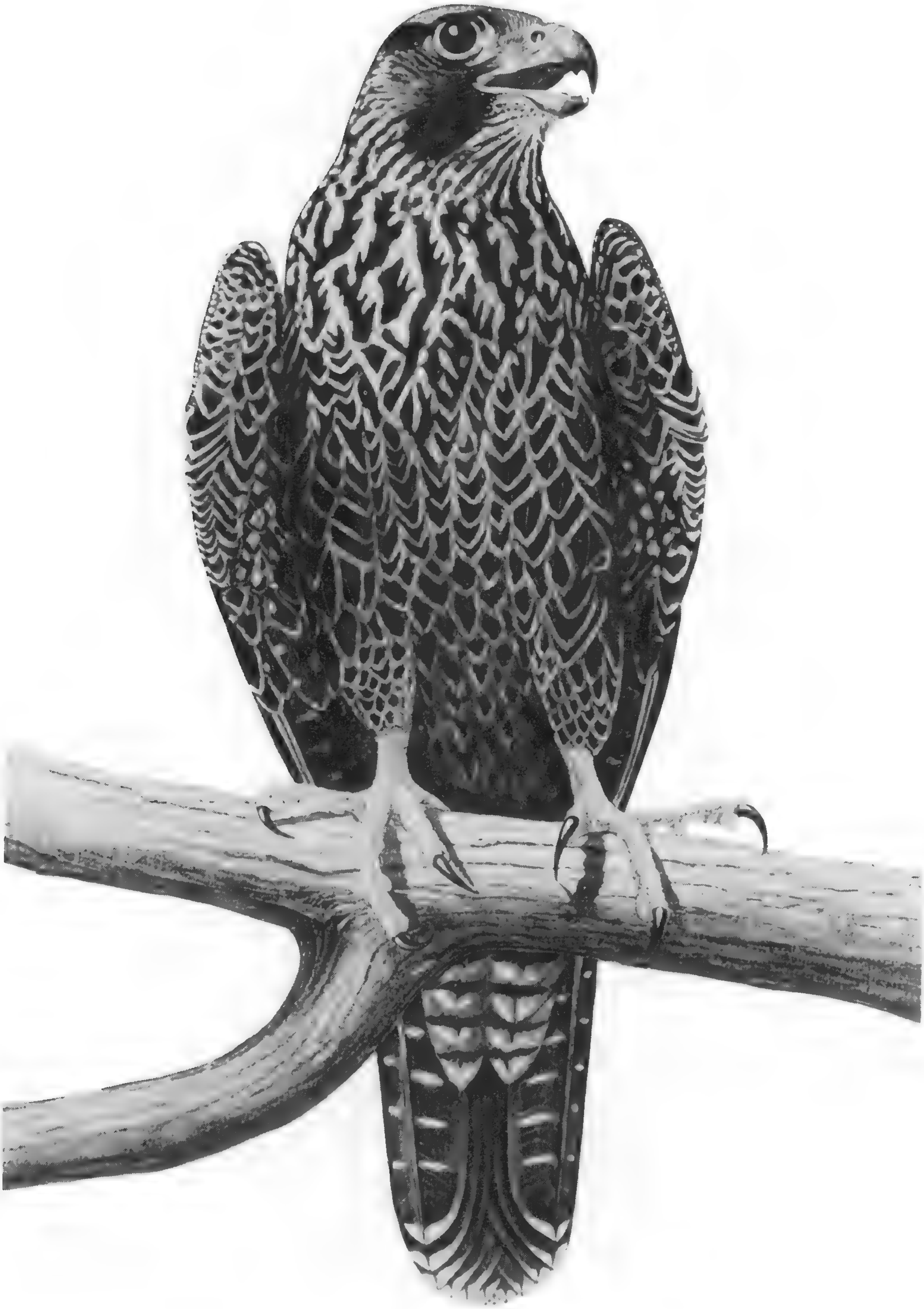

Immature Peregrine Falcon, *Falco peregrinus.* Painting by Heinz Meng.

ORGANIZATION OF A TROPICAL NECTAR FEEDING BIRD GUILD IN A VARIABLE ENVIRONMENT

JEAN-LUC DES GRANGES

Hummingbirds and other nectar-feeding birds exploit a common resource in similar fashion and thus constitute a guild (Root 1967). In this paper I will examine the fluctuations of hummingbird resources and how the competitive interactions among hummingbirds affect the structure of the nectarivorous guild. Even though hummingbirds supplement their diet with arthropods, most of them are highly dependent on nectar for energy. Nectar represents a relatively rich, potentially predictable, and usually renewable resource that can be subdivided competitively in a number of ways among exploiting species. Its ease of characterization and the ease of observing birds feeding at nectar sources make the energetic interaction between plants and birds useful for studies of foraging strategies (Snow and Snow 1972; Wolf 1970; Wolf *et al.* 1976) and community organization of nectar-feeding birds (Feinsinger 1976; Ford and Paton, in press).

Given data on resource exploitation patterns, one can determine the actual niche position and breadth, and the overlap between the different species, along the diet axis. Shifts in these values between seasons of variable food supply and different competitive assemblages should reflect important aspects of the guild's organization. In this paper, I will explore how nectar availability and interspecific competition influence flower visitation and the seasonal occurrence of the different hummingbird species. In another paper (DesGranges and Grant, in press), the problem of how migrant hummingbirds fit into tropical communities is studied in greater detail. Hence the two papers are complementary, although they overlap to a small extent.

Study Area

I selected Volcan de Colima, Mexico (Lat. 19° N) and its surrounding region for this research (Figures 1 and 2). The locality contains many different habitats within a reasonable distance, and supports several hummingbird species, including most of those that migrate from North America for the winter. The varied vegetative cover is partly determined by the extremely varied physiographic conditions in the region. The relief goes from sea level to 4,270 meters in less than 60 air-line kilometers (Figure 3).

The area is subjected to three types of climate. In the coastal plain, a

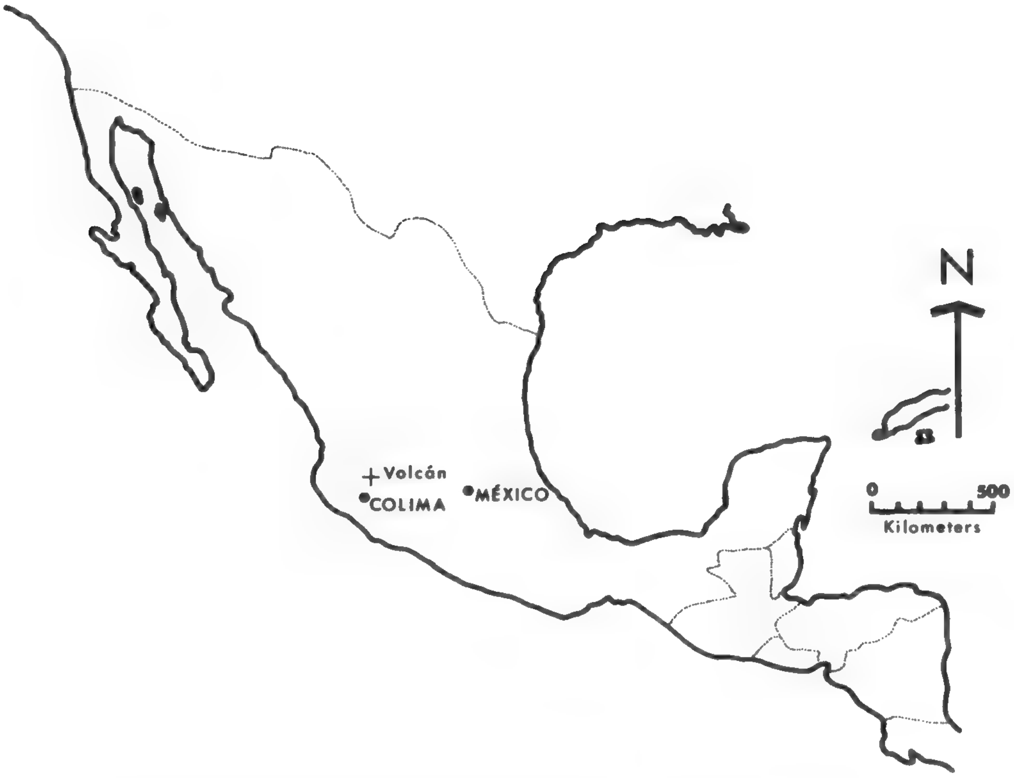

Figure 1. Map of Mexico showing the location of Volcán de Colima.

humid tropical climate prevails; at intermediate altitudes it is a sub-humid tropical climate; and a humid mesothermal climate prevails at high altitude (Thornthwaite 1931). A dry season lasts from November to the middle of June and is notable for its long succession of clear, cloudless, warm days. During the wet season, from the middle of June to October, brief but torrential rains fall almost daily. The humidity reaches an average of 85 percent and the temperature reaches 30°C. The higher slopes of the mountain are quite cold throughout the year, with snow often mantling the top in January and February.

Schaldach (1963), following Leopold (1950), presents an interesting discussion of vegetation zones found in the State of Colima. I will limit myself to habitats where I collected data. Along the altitudinal gradient, the four selected habitats are: arid thorn forest at 485 meters from sea level, riparian gallery forest at 530 meters, arid pine-oak forest at 2,200 meters, and humid pine-oak forest at 3,300 meters (Figures 3 and 4).

The arid thorn forest is found at low elevation in relatively open situations. It consists of flowering trees, mostly legumes and cacti, scattered in a thick undergrowth of thorny vines. This forest is deciduous. Flowering occurs mainly in the dry season when the branches are bare of leaves. Characteristic genera are: *Acacia, Ceiba, Exogonium, Lemairocereus*, and *Mimosa*. The riparian gallery forest is found along streams at a higher altitude. It is a thin, more or less open, but heavily shaded forest of tall trees, many of which are evergreen. The characteristic genera represented in this formation are *Bumelia, Calliandra, Enterolobium, Ficus, Inga, Paullinia*, and *Psittacanthus*. The arid pine-oak forest is an open, dry forest of tall pines and medium sized oaks. This habitat covers extensive areas on the mountain between 1,500 and 2,500 meters. Characteristic genera are *Cirsium, Fuchsia, Leonotis, Lippia, Lobelia, Malvaviscus, Phaseolus, Pinus, Quercus*, and *Salvia*.

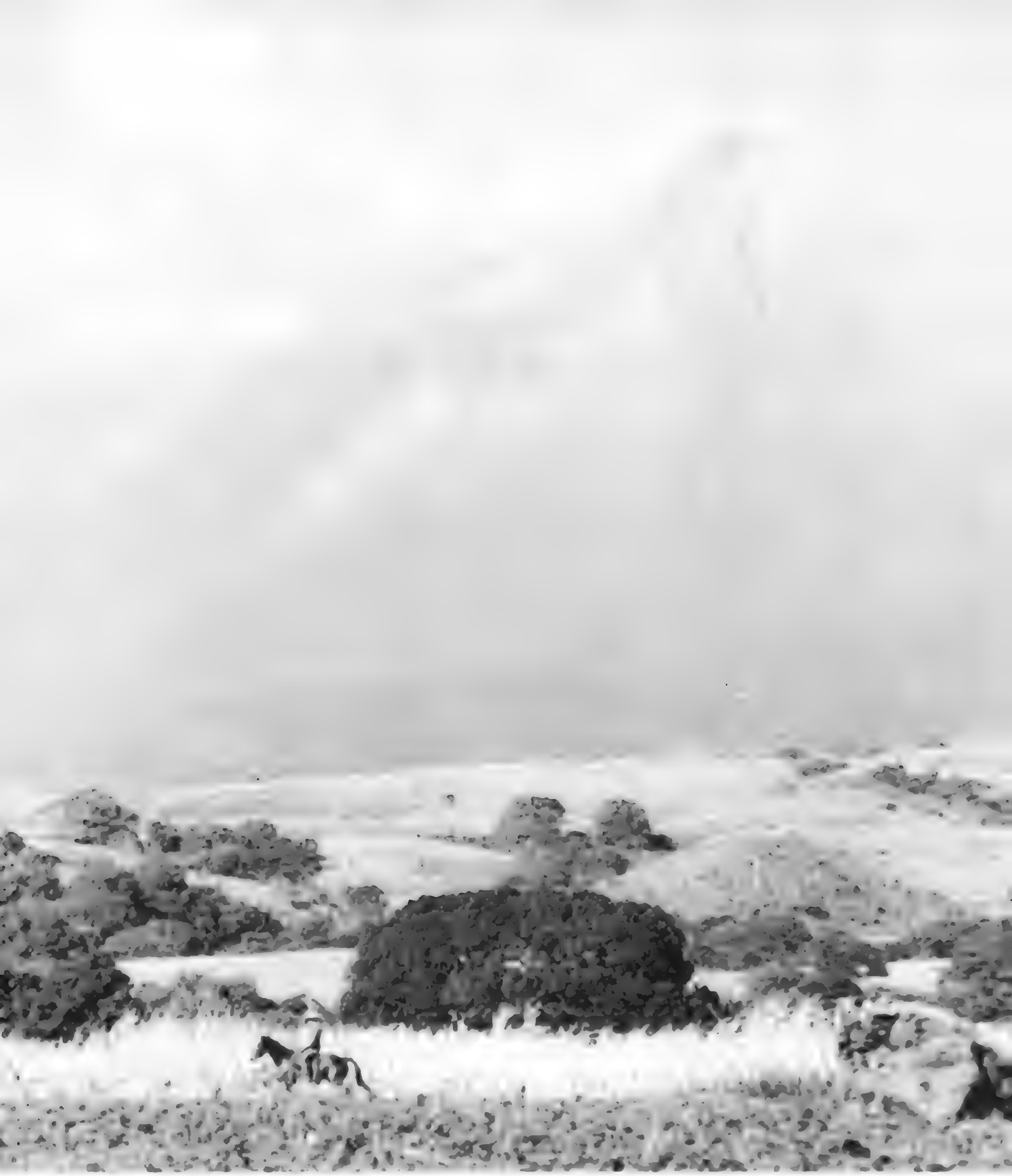

Figure 2. The enormous massif of twin volcanoes dominating the northern border of the State of Colima and adjacent Jalisco are known collectively as the Volcán de Colima. The higher peak is called the Volcán de Nieve (4,264 meters), the lower peak, an active crater, is the Volcán de Fuego (3,600 meters). Photograph taken in January (from DesGranges and Grant, in press).

Humid pine-oak forest occurs above 2,500 meters, where clouds lie against the mountain sides. It is a wetter and denser forest than the lower ones. Oaks are heavily covered with mosses. The characteristic genera represented in this formation are *Buddleia*, *Cestrum*, *Cirsium*, *Penstemon*, *Pinus*, *Quercus*, *Ribes*, *Senecio*, and *Symphoricarpos*. Around human settlements, several ornamental and fruiting trees are often visited by hummingbirds. These include *Caesalpinia*, *Coffea*, *Jacaranda*, *Murraya*, and *Musa*. Because of the great importance of these "oases" for hummingbirds during summer, some data were collected during that season in a garden near the riparian gallery forest transect.

Methods

During eight months (Table 1), spread over a little more than an annual cycle (January 1975, May to July 1975, and October 1975 to February 1976), I spent nearly 700 hours of observation collecting some 35 hours of foraging data on 21 hummingbird species found in the five study areas. The selected habitats are representative of the ones frequented by local hummingbirds. All data were gathered along one-kilometer transects in each habitat, except for the garden, where observations were made randomly where flowers were present.

The work was divided into one-month blocks. During a typical month, one week was spent in each habitat censusing hummingbirds during the morning and late afternoon and collecting botanical data during the afternoon. Mist-nets were set occasionally, and, before being released, hummingbirds were marked with a unique combination of spots painted on the back (Stiles and Wolf 1973).

Censuses were conducted by walking slowly back and forth (three times, two km each day) along the transects, identifying the species of each hummingbird encountered and noting the individual identity of any marked bird. Usually a census lasted for two and one half hours. Two observers (Daniel Bordage or Benoit Houde, and myself) recorded data simultaneously in different sections of the transect. Observations made by the different observers were comparable. By following movements of hummingbirds, as well as by noting location of territories, we were able to make good estimates of the number of individuals of each species found along the one-kilometer transects at different times of the year. The average number of birds encountered per visit in each season should then constitute acceptable measures of density. Each time a hummingbird visited a flower, we noted the species, sex, and marks if any. In addition, data were collected on habitat, height of feeding, and food eaten (nectar or arthropods), and conspicuousness of flowers—that is, whether inside or outside the vegetation as well as the degree of flower clumping at place of feeding. Time and duration (using a stop-watch) of foraging, number of flowers visited during the foraging bout, and evidence of competition as shown by aggressive and territorial behavior were also recorded. A hummingbird was considered to be territorial if it remained in the immediate vicinity of one or more clumps of flowers for at least half an hour, and if, during this time, it fed at the clump and attempted to prevent other hummingbirds from doing so by threatening or attacking them (Wolf 1969). Finally, we noted whether the bird was hovering or sitting while feeding.

Sometimes we selected for observation a representative clump of a plant species at the peak of flowering. Here we recorded the time it took for territory holders and intruders to empty flowers of nectar. In addition, we noted where the birds were feeding in the territories. On one occasion, we recorded the sequence of visits and the time between subsequent visits at marked flowers for which the volume of nectar present in the corolla could be estimated from a curve of the rate of nectar production.

I weighed each hummingbird caught to 0.25 grams, then measured to 0.1 millimeters with calipers the length of exposed culmen, depth and width of bill, wing chord, and total body length. When possible, I recorded sex and age of the bird. Techniques in Stiles (1971, 1972) were very useful with migratory species. Samples were increased to about ten individuals of each species (half males and half females) with museum specimens and with published data in Stiles (1971) and Peterson and Chalif (1973). These supplementary measurements were comparable to mine.

I collected specimens of each of the hummingbird-exploited flowers for later identification. At the same time, I recorded types, abundance of flowers, and distances between flowers

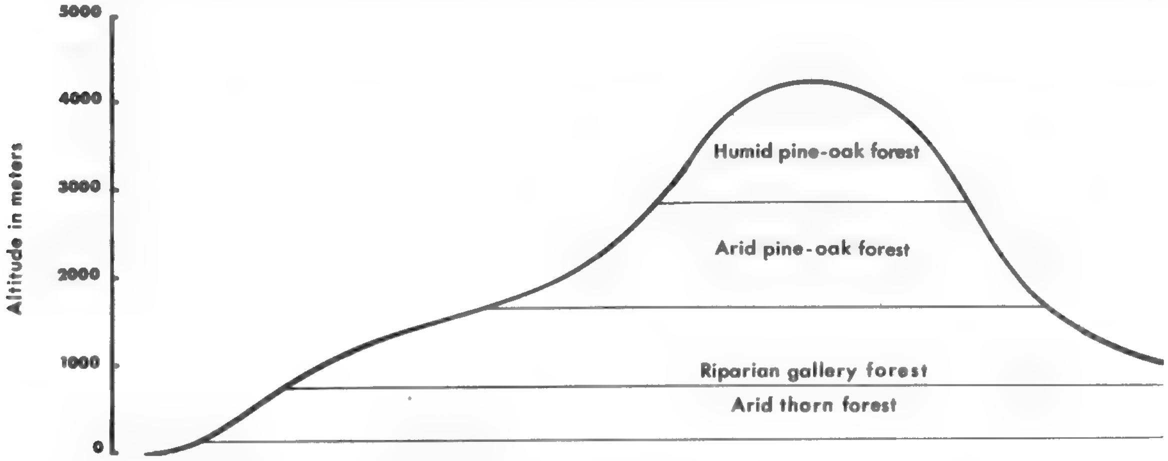

Figure 3. Altitudinal gradient showing the location of the four selected habitats.

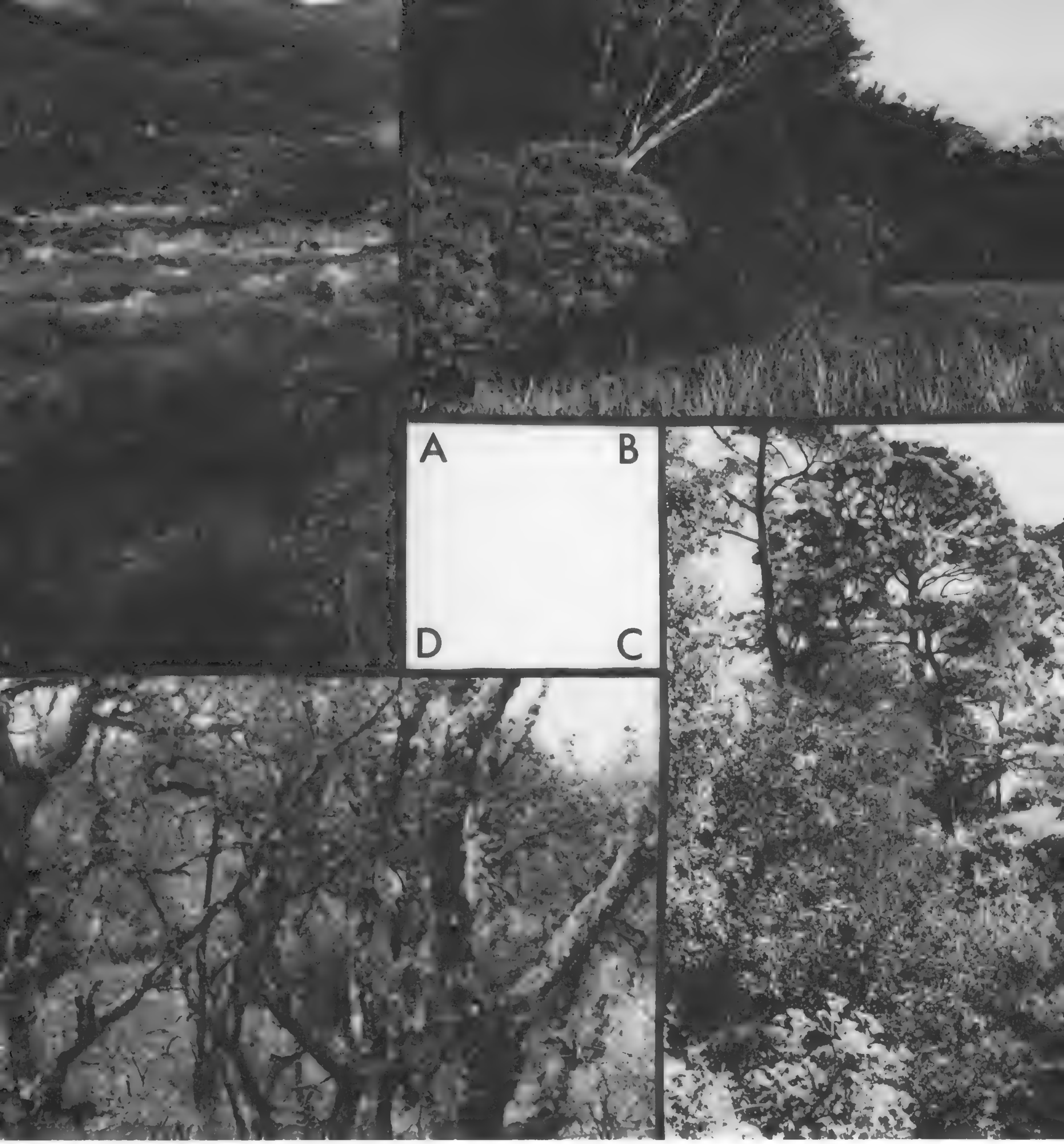

Figure 4. Photographs taken in the four study habitats. A: Arid thorn forest in January. B: Riparian gallery forest in February. C: Arid pine-oak forest in December. D: Humid pine-oak forest in November.

and inflorescences, together with the color and morphology of flowers (i.e., corolla length and diameter), nectar concentration (using a pocket refractometer), the presence of insects and volume of nectar in flowers bagged with cheese cloth for 24 hours to prevent bird and insect visits, and in non-bagged flowers using a comparative spotting technique. The comparative spotting technique consists of first squeezing the corolla and spotting the drop of nectar from the flower on a piece of filter paper, and then comparing the size of the spot obtained with a reference series of spots of different sizes obtained in a comparable way from drops of sucrose solution (20% sugar concentration) of known volume. This was done each month in each habitat. In most instances, I sampled ten flowers of each species selected non-systematically along the transect, but sometimes my sample size was as large as 25 flowers. I measured distances between flowers and inflorescences smaller than 10 centimeters with calipers and estimated larger ones. Flower numbers were either counted along the whole one-kilometer transect or estimated by stratified random sampling (one 10-meter transect per 100-meter section of the one-kilometer transect) when abundant. On these occasions, I counted in tens or hundreds and then extrapolated from the number of flowers in a subsample. Nectar samples which had been spotted on sheets of filter paper for volume determination were air dried and analyzed in the laboratory using Immers' technique (Immers 1964) for the estimation of sugars. Most of the methods used in this study are described in detail elsewhere (Feinsinger 1976; Hainsworth and Wolf 1972; Watt *et al.* 1974).

Percival (1965) mentions that nectar secretion decreases from the first day of bloom and that it is greater during sunny days. In addition, the concentration of sugar in the nectar increases with temperature and decreases with humidity and soil moisture. Therefore it is obvious that the nectar characteristics of a flower species are dependent upon microhabitats and altitude. For these reasons, I used only three classes of nectar production, defined as the ratio of average volume of nectar found in bagged flowers to that in unbagged flowers at midday. When this ratio was less than 1.5, the productivity was classified as low. When the ratio was between 1.5 and 2.5, the productivity was medium. Finally, when the ratio was greater than 2.5, the productivity was high. Similarly, I recognized only three classes of sweetness. Sweetness was low when the average sugar concentration of the nectar of a species was less than 10 percent, medium when the concentration was between 10 and 20 percent, and high when it was greater than 20 percent. These subdivisions are reasonable, since in bird flowers the nectar is usually dilute, with usual concentrations lying between 15 and 25 percent (Heinrich 1975).

Since most flower species change from season to season, I used a cluster analysis to group flowers that are similar in morphology, dispersion pattern, and nectar characteristics. This permits comparisons of resources at different seasons. For the calculation of dissimilarities between flower species, I used the centroid distance measure (Sokal and Michener 1958), which is especially designed for use with morphological attributes.

To describe the diversity of a hummingbird community and the diversity of nectar, I used Shannon's function (Shannon and Weaver 1963). This expression is

$$H' = -\sum_{i=1}^{s} P_i \log_{10} P_i$$

where P_i is the proportion of individuals in the ith hummingbird species ($i = 1, 2, \ldots, s$), or the proportion of the total volume of nectar in the ith flower species. This measure has two separate components, species richness *(s)* and the equitability or evenness of species abundance (Lloyd and Ghelardi 1964). Species richness is simply the number of species in the sample. To measure the relative abundance component, I used the index $J' = H'/H'$ max in which H' max is $\log_{10} s$. This index represents the ratio of the observed diversity to the maximum diversity possible for the same number of species. It has a maximum value of unity when all species are equally abundant. Since the components of the Shannon formula can vary independently of one another, it is obvious that two samples having identical H' values may in fact be very different. Therefore, I will resolve the formula into its components for analysing diversity patterns.

I calculated values of niche breadth and niche overlap using equations 21 and 24 of Colwell and Futuyma (1971). Resource matrices consisted of total amount of time each species of hummingbird spent feeding at each of the flower species of a transect during a period of the year. Ideally, the weighting factors used to compute the weighted niche metrics should be derived anew for each value by skipping the row (for niche breadth) or rows (for niche overlap) for which the metric is to be calculated. Unfortunately, this leads to mathematical complications with matrices smaller than 3 × 2. Because several of my resources matrices were that small, I used the entire set of bird species in the calculation of the resource-state weighting factors. Surprisingly, this had only a moderate effect on final results. Metrics calculated with and without the proposed procedure were highly correlated ($r > .95$, $p < .01$). Unweighted and weighted metrics are also highly correlated (Sabath and Jones 1973). Nevertheless, it is more appropriate to use absolute weighted measures for comparisons among species when resource matrices have different ecological ranges (Colwell and Futuyma 1971).

The Flowers

Flowering of most species was restricted to a particular season, with the long dry season having the greatest number of species in flower (Figure 5). Although the dry season begins in November, appreciable flowering did not begin until December. This major flowering period of the dry season persisted until the middle of February. At the onset of the rainy season in June, there was a pronounced, but brief, period of flowering. After this early rainy season peak, flowering activity dropped off sharply, with only a few species

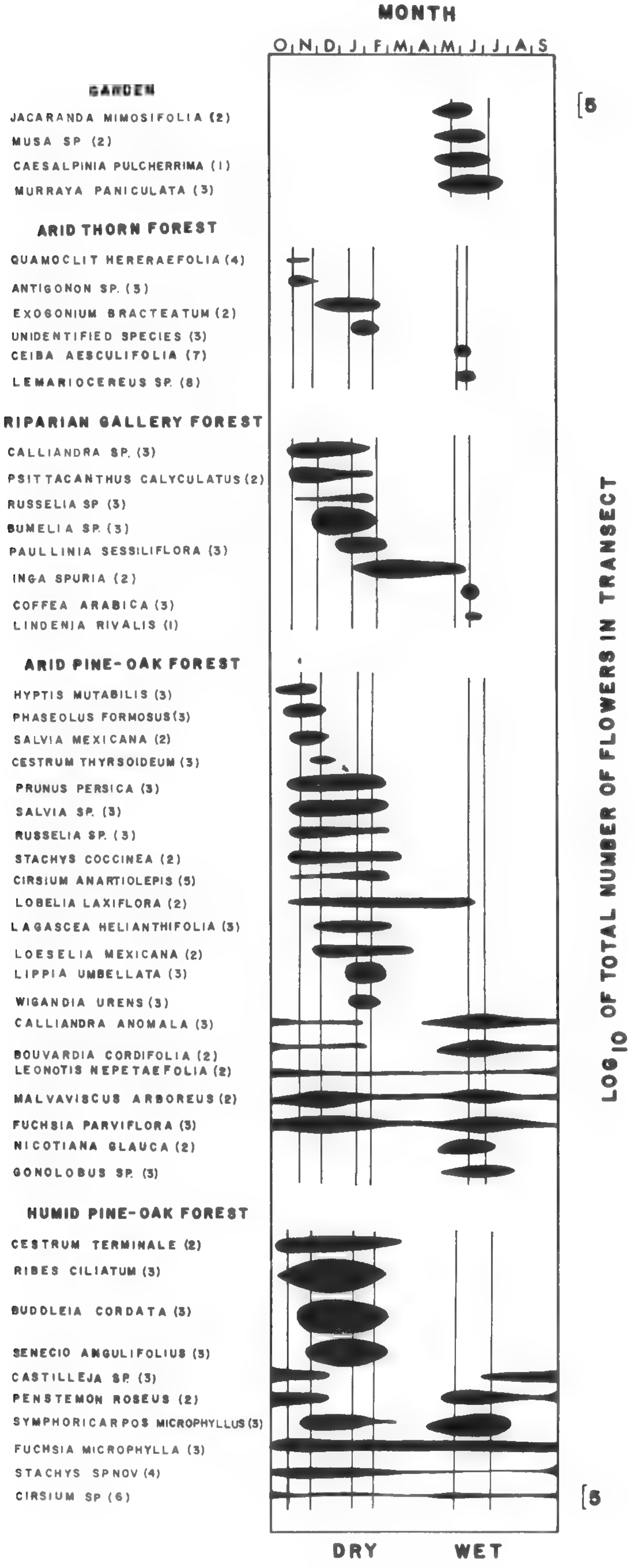

Figure 5. Blooming seasonality of plant species visited by hummingbirds. The vertical axes indicates census dates, and show abundance as $\log_{10}$ of total number of flowers in the transect. The number in parentheses which follows the species name is the number of the cluster to which the species belongs (from DesGranges and Grant, in press).

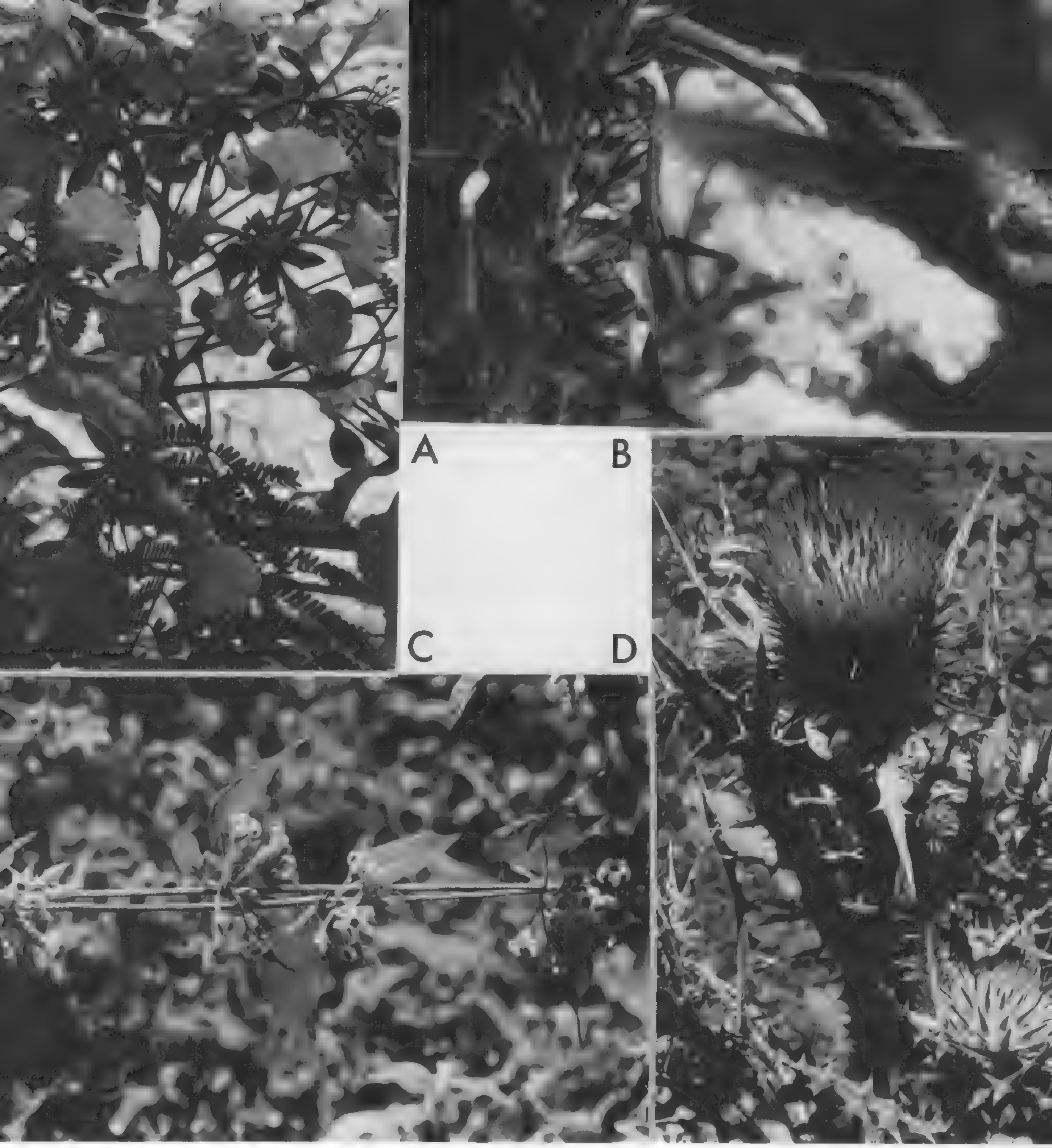

Figure 6. Photographs of typical species of flowers. A: *Caesalpinia pulcherima*. B: *Loeselia mexicana*, a tubular flower. C: *Gonolobus* sp.; a cup-shaped flower; D: *Cirsium* sp.

having their flower peak in July. This flowering sequence is in accord with other phenological investigations of flowering activity conducted in the neotropics (Frankie *et al*. 1974; Janzen 1967a; Leck 1972).

Two clusters contain nearly 85 percent of the species. The first one groups flowers with a fairly long and more or less tubular corolla. The flowers which are usually reddish in color produce a fair amount of nectar. The inflorescences contain relatively few flowers, so that each type is rarely abundant in the habitats. I will call them tubular flowers. The second cluster groups flowers with either relatively flat, open corollas or cup-shaped corollas. The flowers which are usually whitish in color produce a small to moderate amount of nectar but their inflorescences contain larger number of flowers, so that each type is usually very abundant in the habitats. I will call them cup-shaped flowers. Baker and Hurd (1968) call them entomophilous flowers because they are mainly pollinated by insects. I could have adopted this term, and used ornithophilous flowers for the tubular flowers which are mainly pollinated by birds; but I prefer to use the more descriptive, interpretation-free names of tubular and cup-shaped flowers.

Because some of the remaining clusters contain flowers of little interest to hummingbirds, it should simplify further discussion if I lump some of these clusters together. Figure 6 shows examples of typical species of certain clusters.

Because of the synchronization of sexual reproduction of trees and shrubs within the dry season, nectar is much more plentiful during the winter than at other times. The increase in nectar from fall to winter is most pronounced in the cup-shaped group (Figure 7).

The Birds

I observed 21 species of hummingbirds in the course of this study (Plate 1, Table 2). Their morphological characteristics are presented in Table 2. Hummingbirds have a very swift and agile flight, and can travel long distances in search of their specialized food. Since the number of flowers available in the various habitats fluctuates continuously during the year (see Figures 5 and 7), most species of hummingbirds readily disperse. Therefore, the species and numbers of individuals which inhabit the communities change continuously during the year (Table 3).

Patterns of Movements

It is possible to group species of hummingbirds on the basis of their strategy of movement. Residents are tropical species which inhabit particular habitats throughout the year. They remain in these habitats even when the number of flowers dwindles. Wanderers nest in tropical regions but,

TABLE 1

Sampling Periods

	Arid thorn forest	*Riparian gallery forest*	*Arid pine-oak forest*	*Humid pine-oak forest*
Arrival of migrants	14 Oct.–10 Dec.*	14 Oct.–10 Dec.	14 Oct.–11 Nov.	14 Oct.–29 Oct.
Mid- winter	11 Dec.–3 Feb.	11 Dec.–3 Feb.	12 Nov.–21 Jan.	30 Oct.–14 Jan.
Departure of migrants	4 Feb.–12 Feb.	4 Feb.–12 Feb.	22 Jan.–12 Feb.	15 Jan.–12 Feb.
End of dry season	18 May–18 June	18 May–18 June	18 May–18 June	18 May–18 June
Beginning of rainy season	19 June–19 July	19 June–19 July	19 June–19 July	19 June–19 July

*Dates chosen coincided with important changes in the total number of hummingbirds in each habitat. For example, migrants are uncommon in the habitats outside the mid-winter period (from DesGranges and Grant, in press).

unlike residents, they are not present all year in a particular habitat. Rather, they visit several habitats during the year, following seasonal blooms of trees and shrubs. Finally, the migrants breed in the north temperate regions during summer and invade the tropical regions during winter. The groups to which species belong are indicated in Table 3. Note that some resident species wander occasionally to take advantage of seasonal abundance of food in neighboring habitats.

In addition to these seasonal movements of populations, there exists, at least during the cold winter, a daily altitudinal migration of hummingbirds at high altitude on the volcano (see Dorst 1956; Swan 1952). Except for the White-eared Hummingbird (see Plate 1 for scientific names of the hummingbirds discussed in this paper),which does not seem to leave the humid pine-oak forest at night, all other species which inhabit this habitat show a very significant movement uphill between 07:00 and 08:00 hours,[1] and a downhill movement after 16:30 hours.[2] The arrival of hummingbirds in the morning is at a maximum in the half-hour following sunrise. As soon as they arrive, the birds start feeding vigorously until about 09:45 hours, when their activity is much reduced. The departure reaches a maximum between 16:30 and 18:00 hours. The larger species leave last and can be seen flying downhill at the time the first stars show in the sky.

Territoriality

Certain species ensure exclusive use of clumps of flowers that produce large quantities of nectar by setting up feeding territories (Feinsinger 1976; Lyon 1976; Pitelka 1942; Wolf *et al.* 1976). For nectar feeders, food is easily visible, stationary, and predictably renewable, thus providing sufficient conditions for specific resource defense rather than spatial defense. Territory holders are conspicuous and aggressive, excluding not only conspecifics but also individuals of other species. In contrast, birds excluded from rich clumps of flowers by territorial individuals, or faced with a spectrum of flowers lacking rich clumps, make use of the dispersed, low yield resources. They exhibit "traplining" behavior (Feinsinger 1976; Janzen 1971); that is, they follow a regular feeding route between successive patches of flowers at low densities on scattered trees, shrubs, vines, and herbs. The contrast between traplining and territorial behavior is not absolute. Birds may exploit dispersed flowers without following regular traplines, and some species employ both strategies regardless of whether they are residents or wanderers (Table 3).

Interspecific territoriality occurred in all three groups of birds. This may appear to be a waste of energy in view of the nectar surplus in certain flowering species and the normally relaxed competition in such cases. Nevertheless, the energy expended in territorial defense may be offset by the gain in reduced foraging time and costs (Wolf *et al.* 1975). It seemed that territorial birds had a good knowledge of flowers they had recently visited. They tended to visit flowers in some sequential order to allow maximal replenishing of nectar. For example, it takes about 55 minutes for an empty flower of *Exogonium bracteatum* to produce 85 percent of its maximum

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[1] d.f. = 1, $X^2 = 15.1$, $p<.01$

[2] d.f. = 1, $X^2 = 46.1$, $p<.01$

TABLE 2

Morphological Characteristics of the Hummingbird Species Studied

	Total length (cm)†	*Body weight (g)*	*Wing length (mm)*	*Wing disc loading* (g/cm^2)	*Exposed culmen (mm)*	*Bill width (mm)*	*Bill depth (mm)*	*Index of bill curvature*‡	*Sexual dimorphism*§
Phaethornis superciliosus (Ph)	15.9 (0.7)	6.1 (0.6)	62.0 (1.6)	0.0353	39.3 (0.1)	4.1 (0.09)	3.7 (0.45)	4	2
Colibri thalassinus (Ct)	11.2 (–)	5.4 (0.2)	63.4 (2.2)	0.0301	19.1 (0.4)	2.3 (0.01)	2.4 (0.30)	2	2
Chlorostilbon canivetii (Cc)	8.3 (0.7)	2.5 (0.3)	45.9 (0.5)	0.0260	14.2 (0.1)	2.5 (0.02)	2.2 (0.02)	2	1
Cynanthus latirostris (Cl)	9.2 (1.0)	3.0 (0.1)	51.6 (1.6)	0.0242	20.4 (0.5)	3.5 (0.00)	2.5 (0.17)	2	1
Hylocharis leucotis (Hl)	8.8 (0.3)	3.8 (0.2)	54.5 (0.7)	0.0277	16.9 (0.3)	3.9 (0.31)	1.9 (0.05)	2	1
Amazilia beryllina (Ab)	9.6 (0.1)	4.6 (0.2)	54.3 (0.8)	0.0340	19.3 (0.9)	2.9 (0.11)	2.4 (0.11)	2	2
Amazilia rutila (Ar)	10.1 (–)	4.8 (0.1)	54.4 (0.9)	0.0359	21.3 (1.0)	3.4 (0.00)	2.6 (0.01)	2	2
Amazilia violiceps (Av)	10.1 (0.4)	5.7 (0.1)	54.8 (0.7)	0.0413	22.3 (0.2)	3.2 (0.02)	2.7 (0.07)	2	2
Lampornis clemenciae (Lc)	11.9 (0.1)	7.5 (0.6)	73.9 (2.2)	0.0312	24.5 (1.8)	2.7 (0.04)	2.7 (0.18)	2	1
Lampornis amethystinus (La)	10.9 (0.1)	5.6 (0.8)	64.9 (3.0)	0.0298	21.1 (1.0)	3.1 (0.06)	2.3 (0.17)	2	1
Eugenes fulgens (Ef)	12.1 (0.7)	8.5 (3.1)	70.0 (2.1)	0.0395	26.1 (1.2)	2.8 (0.50)	2.4 (0.30)	2	1
Heliomaster constantii (Hc)	11.2 (–)	7.8 (0.1)	62.9 (1.3)	0.0413	34.2 (0.9)	3.6 (0.16)	2.9 (0.10)	1	2
Tilmatura dupontii (Td)	7.6 (1.3)	2.3 (0.1)	34.6 (0.2)	0.0399	12.9 (0.3)	1.9 (0.09)	1.5 (0.11)	2	1
Calothorax lucifer (Clu)	9.3 (–)	2.9 (0.2)	39.6 (1.3)	0.0387	20.3 (0.1)	1.9 (0.06)	2.2 (0.05)	3	1
Archilochus colubris (Ac)	8.5 (0.3)	3.1 (0.1)	42.0 (2.8)	0.0376	16.4 (1.2)	1.7 (0.01)	1.7 (0.23)	2	1
Archilochus alexandri (Aa)	8.5 (0.3)	3.3 (0.1)	44.1 (1.9)	0.0353	19.6 (1.2)	1.7 (0.01)	1.7 (0.23)	2	1
Stellula calliope (Sc)	7.4 (0.3)	2.7 (0.2)	40.1 (1.5)	0.0358	14.9 (0.7)	2.1 (0.10)	1.3 (0.09)	2	1
Atthis heloisa (Ah)	6.9 (–)	2.2 (0.3)	36.8 (0.2)	0.0343	12.2 (0.1)	1.4 (0.21)	1.5 (0.04)	2	1
Selasphorus platycercus (Sp)	8.9 (0.1)	3.6 (0.2)	49.8 (0.7)	0.0320	18.0 (0.7)	2.3 (0.11)	1.5 (0.01)	2	1
Selasphorus rufus (Sr)	8.2 (0.1)	3.2 (0.2)	42.4 (2.0)	0.0381	16.8 (0.8)	2.0 (0.02)	1.7 (0.08)	2	1
Selasphorus sasin (Ss)	7.6 (–)	3.6 (0.2)	40.8 (2.4)	0.0450	19.1 (0.8)	1.8 (0.41)	1.8 (0.03)	2	1

*Means are calculated from the means of each of the two sexes. Standard error is given in parentheses when available.

†Data in Peterson and Chalif (1973), Robbins *et al.* (1966), and Stiles (1971) were used when my own data were insufficient.

‡1 = straight bill, 2 = slight bill curvature, 3 = medium bill curvature, 4 = large bill curvature.

§1 = well pronounced sexual dimorphism, 2 = not pronounced sexual dimorphism.

TABLE 3

Status and Abundances of Hummingbird Species Constituting the Nectarivorous Bird Guild in the Study Habitats

Species in each habitat	*Vagility**	*Territoriality†*	*Density per time period‡*					*Seasonal abundance§*				
			1	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
Garden:												
Chlorostilbon canivetii	W	Tr	—	—	—	4.0	1	—	—	—	25	50
Amazilia beryllina	W	Tr	—	—	—	1.0	—	—	—	—	6	—
Amazilia rutila	W	Te	—	—	—	10.0	1	—	—	—	63	50
Amazilia violiceps	W	Tr	—	—	—	1	—	—	—	—	6	—
Arid Thorn Forest:												
Chlorostilbon canivetii	W	Tr	2.0	—	—	—	—	21	—	—	—	—
Cynanthus latirostris	R	Te	3.0	6.7	9.0	2.0	1.5	31	35	36	44	100
Amazilia beryllina	W	Te	—	0.2	—	0.3	—	—	0.9	—	6	—
Amazilia rutila	W	Tr	—	0.2	0.5	—	—	—	0.9	2	—	—
Amazilia violiceps	W	Tr	—	3.3	0.5	0.8	—	—	18	2	17	—
Heliomaster constantii	R	Tr	4.0	0.8	2.0	1.5	—	42	4	8	33	—
Calothorax lucifer	W	Te	—	4.5	7.5	—	—	—	24	30	—	—
Archilochus sp.	M	Te	0.5	1.2	1.5	—	—	6	6	6	—	—
Selasphorus platycercus	W	Te	—	0.8	2.0	—	—	—	5	8	—	—
Selasphorus rufus	M	Te	—	1.2	2.0	—	—	—	6	8	—	—
Riparian Gallery Forest:												
Phaethornis superciliosus	W	Tr	—	—	—	0.4	—	—	—	—	4	—
Chlorostilbon canivetii	R	Tr	3.5	3.2	4.0	4.0	0.7	38	20	19	40	40
Cynanthus latirostris	W	Tr	1.7	1.2	5.0	—	—	18	8	24	—	—
Amazilia beryllina	W	Te	0.1	1.5	3.0	—	—	1	10	14	—	—
Amazilia rutila	R	Te	2.5	3.0	5.0	5.5	1.0	27	20	24	56	60
Amazilia violiceps	W	Tr	0.1	0.2	—	—	—	1	1	—	—	—
Heliomaster constantii	W	Tr	0.2	—	—	—	—	3	—	—	—	—
Tilmatura dupontii	W	Tr	—	—	1.0	—	—	—	—	5	—	—
Archilochus sp.	M	Te	1.1	6.2	3.0	—	—	12	40	14	—	—
Selasphorus platycercus	W	Te	—	0.2	—	—	—	—	1	—	—	—

TABLE 3 (continued)

Species in each habitat	*Vagility**	*Territoriality†*	*Density per time period‡*					*Seasonal abundance§*				
			1	*2*	*3*	*4*	*5*	*1*	*2*	*3*	*4*	*5*
Arid Pine-Oak Forest:												
Hylocharis leucotis	R	Te	6.8	5.5	7.0	8.0	3.0	41	27	26	65	24
Amazilia beryllina	R	Te	2.7	3.7	3.0	2.0	4.7	16	18	11	16	38
Lampornis clemenciae	W	Tr	1.0	—	—	—	—	6	—	—	—	—
Lampornis amethystinus	W	Tr	1.5	0.1	—	1.7	3.7	9	0.2	—	14	30
Eugenes fulgens	R	Tr	0.3	1.0	2.3	P¶	0.3	4.5	5.0	8.0	—	5
Calothorax lucifer	W	Tr	—	0.1	0.3	—	—	—	0.4	0.9	—	—
Stellula calliope	M	Te	0.3	3.8	0.8	—	—	4.5	19	3	—	—
Atthis heloisa	W	Tr	—	—	—	0.7	0.7	—	—	—	5	5
Selasphorus platycercus	W	Te	3.3	6.0	13.5	—	—	20	27	50	—	—
Selasphorus rufus	M	Tr	0.8	0.2	—	—	—	5	0.8	—	—	—
Selasphorus sasin	M	Tr	—	—	0.3	—	—	—	—	0.9	—	—
Humid Pine-Oak Forest:												
Colibri thalassinus	W	Te	—	12.8	8.0	—	—	—	20	17	—	—
Hylocharis leucotis	R	Te	9.5	7.6	8.0	5.2	4.0	81	12	17	75	100
Amazilia beryllina	W	Tr	—	—	—	0.04	—	—	—	—	0.5	—
Lampornis amethystinus	W	Tr	0.7	—	—	—	—	6	—	—	—	—
Eugenes fulgens	R	Tr	1.3	1.6	2.0	1.7	P	10	2	4	24	—
Stellula calliope	M	Te	—	0.4	0.5	—	—	—	0.6	1	—	—
Selasphorus platycercus	W	Te	0.3	13.8	16.7	—	—	3	22	35	—	—
Selasphorus rufus	M	Te	—	10.4	1.0	—	—	—	16	2	—	—
Selasphorus sasin	M	Te	—	0.1	—	—	—	—	0.2	—	—	—
Selasphorus sp.	M	Te	—	16.9	12	—	—	—	27	25	—	—

Note: From DesGranges and Grant, in press.

*R = resident, W = wanderer, M = migrant.

†Te = territorial, Tr = trapliner.

‡Density is the average number of individuals seen along a transect during a census, 1 = arrival of migrants, 2 = mid-winter, 3 = departure of migrants, 4 = end of dry season, 5 = beginning of rainy season.

§Seasonal abundance is the percent of the individuals of a guild which are of a certain species.

¶Present but not seen during the censuses.

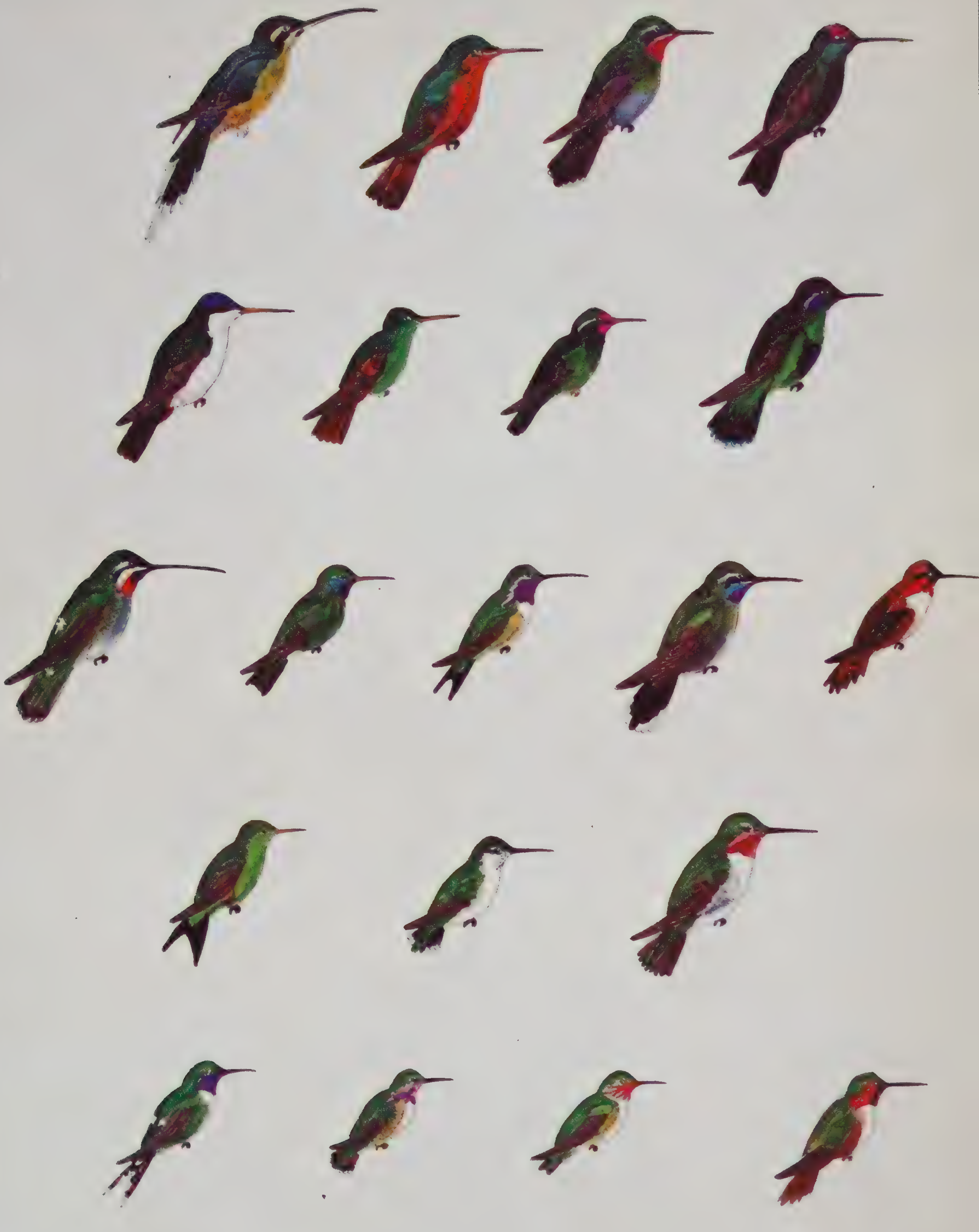
volume of nectar. Thereafter, further replenishment is very slow (Figure 8). With marked flowers, it was found that a territorial male Broad-billed Hummingbird revisited a particular flower every 51.2 minutes on the average ($n = 6$, $S\bar{x} = 9.3$), while intruders were often visiting flowers recently emptied by the territorial holder (see Gill and Wolf 1975).

It was clear that dominant species monopolized most of the territories full of flowers, although I did not collect systematic data to substantiate this phenomenon. Subordinate species defended marginal territories, if at all, with fewer flowers that were often less productive and more dispersed. But due to the staggering of the blooming period of the different plant species (see Figure 5), the attractiveness of a territory varies and the location of territories as well as territory holders changed regularly with time. Most migratory species had a low status of dominance. I often observed that certain marked individuals left their territories when they became richer in nectar, leaving dominant competitors to occupy the territories. Exclusion probably occurred, but was not witnessed. The displaced birds then moved to marginal territories and remained there until they became good territories (i.e., rich in nectar resources) and attracted superior competitors.

Behavioral Interactions

Belligerence was general in all species studied and was more accentuated when several individuals were gathering at flowering trees (see Stiles and Wolf 1970). Chases between the sexes and among several species occurred when they were on common feeding grounds (Table 4). Thus, it is possible to construct a hierarchy according to relative dominance in interspecific interactions. Dominant hummingbirds (Plate 1, top row) win most of their interspecific chases. At the other extreme are species which lose most of their interspecific chases (Plate 1, bottom row). Species on the same row in Plate 1 are about equally successful in their interspecific chases against each other while they lose more than 60 percent of their chases with species ranked higher in the hierarchy, and win more than 60 percent of their chases against species found below them in the hierarchy. Obviously, certain species never encounter each other because of habitat segregation. Nevertheless, using their performance against common competitors, they can be ranked in relation to each other. In general, residents are dominant, although the Fork-tailed Emerald is subordinate to most species. Wanderers usually have

Plate 1. Plate of the hummingbird species studied. They are displayed according to their status in a hierarchy of dominance in interspecific interactions. Unless specified, the illustration indicates that male and female are similar. First row, very high dominance: Long-tailed Hermit ♂ *(Phaethornis superciliosus)*, Cinnamon Hummingbird *(Amazilia rutila)*, Amethyst-throated Hummingbird ♂ *(Lampornis amethystinus)*, Rivoli's Hummingbird ♂ *(Eugenes fulgens)*. Second row, high dominance: Violet-crowned Hummingbird *(Amazilia violiceps)*, Berylline Hummingbird *(Amazilia beryllina)*, White-eared Hummingbird ♂ *(Hylocharis leucotis)*, Green Violet-ear *(Colibri thalassinus)*. Third row, intermediate dominance: Plain-capped Starthroat ♂ *(Heliomaster constantii)*, Broad-billed Hummingbird ♂ *(Cynanthus latirostris)*, Lucifer Hummingbird ♂ *(Calothorax lucifer)*, Blue-throated Hummingbird ♂ *(Lampornis clemenciae)*, Rufous Hummingbird ♂ *(Selasphorus rufus)*. Fourth row, low dominance: Fork-tailed Emerald ♂ *(Chlorostilbon canivetii)*, Ruby-throated and Black-chinned Hummingbirds ♀ *(Archilochus colubris* and *A. alexandri)*, Broad-tailed Hummingbird ♂ *(Selasphorus platycercus)*. Fifth row, very low dominance: Dupont's Hummingbird ♂ *(Tilmatura dupontii)*, Bumblebee Hummingbird ♂ *(Atthis heloisa)*, Calliope Hummingbird ♂ *(Stellula calliope)*, Allen's Hummingbird ♂ *(Selasphorus sasin)* (from DesGranges and Grant, in press).


PETER LANE

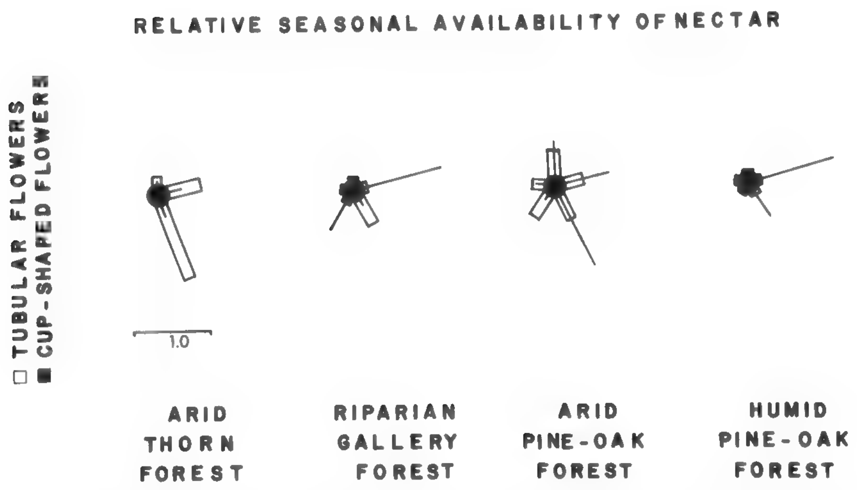


Figure 7. Relative seasonal availability (RSA) of nectar in tubular and cup-shaped flowers during the five time periods in each of the four habitats. RSA in the amount of nectar (A) in flower type *(j)* in habitat *(h)* during time period *(t)* expressed as a proportion of the maximum amount of nectar found in either of the two flower types in that habitat during any period of the year, (i.e. $RSA_{jht} = A_{jht}/\text{maximum } [A_{jht}]; t = 1,5; j = 1,2$). Arms of the stars represent periods of the yearly cycle with the arrival of migrants at the top and, in clockwise progression, mid-winter, departure of migrants, the end of the dry season, and the beginning of the rainy season (from DesGranges and Grant, in press).

a high dominance status and are mostly trapliners.[3] Finally, north temperate migrants are territorial and have a low dominance status, with the exception of the Rufous Hummingbird.[4] A canonical correlation analysis showed that birds of large size (using several meristic measurements) tend to be sedentary and dominant while smaller birds tend to be highly vagile and subordinate.[5] Contrary to the usual pattern (see Skutch 1973), bill size and length of the corolla of the preferred flowers were not correlated, although species with curved bills tended to feed from larger flowers.[6]

For each one of the 17 winner species (Table 4), we can look at the three species most often encountered aggressively. In doing so, we find that conspecifics are represented with 15 of the 17 species. In addition, we note that heterospecifics which are most often chased rarely belong to the same group (i.e., residents, wanderers, or migrants) as the attacking species.[7]

Conspecifics obviously share a common niche and are thus in perpetual competition. Some species are almost continuously in the presence of one another—residents because of their fidelity to a habitat, and wanderers and migrants because of their synchronized travels. These prolonged contacts are favorable to the coadjustment of the niches of the species of a group and should lead to the ecological segregation of each one. It is thus not surprising that within each group, the species do not interfere very much. However, species in different groups meet each other only sporadically and are thus not subjected to identical selective forces. Their niches have not coevolved and they probably overlap to an intolerable degree. Intergroup competition is therefore very accentuated.

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[3] d.f. = 1, $X^2 = 14.1$, $p < .005$

[4] d.f. = 1, $X^2 = 3.6$, $p < .07$

[5] d.f. = 35, canonical $r = .93$, $p = .003$

[6] d.f. = 19, $r = 46$, $p < .05$

[7] d.f. = 1, $X^2 = 16.9$, $p < .005$

TABLE 4

Aggressive Encounters with a Clear Winner

Winner	*Loser*																		*Percentage of intraspecific encounters*
	Ct	*Cc*	*Cl*	*Hl*	*Ab*	*Ar*	*Av*	*Lc*	*La*	*Ef*	*Hc*	*Clu*	*Asp*	*Sc*	*Sp*	*Sr*	*Ss*	*Td*	
Ct	3	—	—	2	—	—	—	—	—	2	—	—	—	—	12	6	—	—	12.0
Cc	—	4	2	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	36.4
Cl	—	5	21	—	—	1	1	—	—	—	—	1	10	—	2	2	—	—	48.8
Hl	2	—	—	47	1	—	—	2	1	2	—	—	—	4	34	6	—	—	46.1
Ab	—	4	16	2	16	2	8	1	—	—	—	1	9	9	4	—	—	—	21.3
Ar	—	3	5	—	4	18	1	—	—	—	—	—	3	—	—	—	—	1	51.4
Av	—	—	7	—	—	—	3	—	—	—	2	2	—	—	4	2	—	—	15.0
Lc	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	50.0
La	—	—	—	—	1	—	—	1	2	—	—	—	—	—	—	—	—	—	40.0
Ef	1	—	—	4	—	—	—	—	1	8	—	—	—	—	4	1	1	—	40.0
Hc	—	—	1	—	—	—	1	—	—	—	6	—	—	—	—	1	—	—	66.7
Clu	—	—	6	—	—	—	—	—	—	—	—	3	—	—	7	4	—	—	15.0
Asp	—	—	2	—	—	—	—	—	—	—	1	2	16	—	4	—	—	—	76.2
Sc	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—	—	100.0
Sp	—	—	1	4	—	—	—	—	—	1	—	2	—	5	105	8	—	—	83.3
Sr	3	—	3	2	—	—	—	—	—	1	—	1	4	1	95	63	1	—	36.2
Ss	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	0.0

Note: The diagonal gives the number of intraspecific chases regardless of outcome. For abbreviations of species names, see Table 2, Asp =*Archilochus* sp.

Species Groups and Habitat

The majority of the species studied live in overlapping geographic ranges, but most of them are partially segregated in their altitudinal ranges and therefore differ in their habitats (Table 3). Moreover, several of these species join the communities at different times of the year so that, at one time or another, the guild of nectarivorous birds in each habitat may comprise as many as ten or eleven species living together. In this section I will describe how the principal coexisting species of each habitat partition the seasonal resources.

Arid Thorn Forest

This semi-desert environment is the harshest of the four habitats studied. Flowers are rare for long periods during the summer and fall. The resident Broad-billed Hummingbirds and Plain-capped Starthroats adjust their diet to feed almost exclusively on insects. At other times of the year, there are rarely more than two plant species flowering at the same time. However, these plants produce a large amount of nectar, which attracts several species of hummingbirds from neighboring habitats or from the north temperate regions.

Hummingbird densities during the January and February flowering period of *Exogonium bracteatum* are up to ten times the summer densities. Wanderers and migrants feed from *Exogonium* opportunistically. Where the flowers are very tightly packed, the abundance of nectar is great enough so that competition is almost non-existent. The two residents also feed from it, but they still continue to feed regularly on insects. Numerous nuptial chases observed at this time of the year suggest that the Plain-capped Starthroat, Broad-billed Hummingbird, and Lucifer Hummingbird are probably nesting. I observed copulation in the Broad-billed Hummingbird during this period.

For a brief period toward the end of the dry season, *Ceiba aesculifolia* and *Lemairocereus* sp. become the new flowers of interest. Unlike *Exogonium*, they

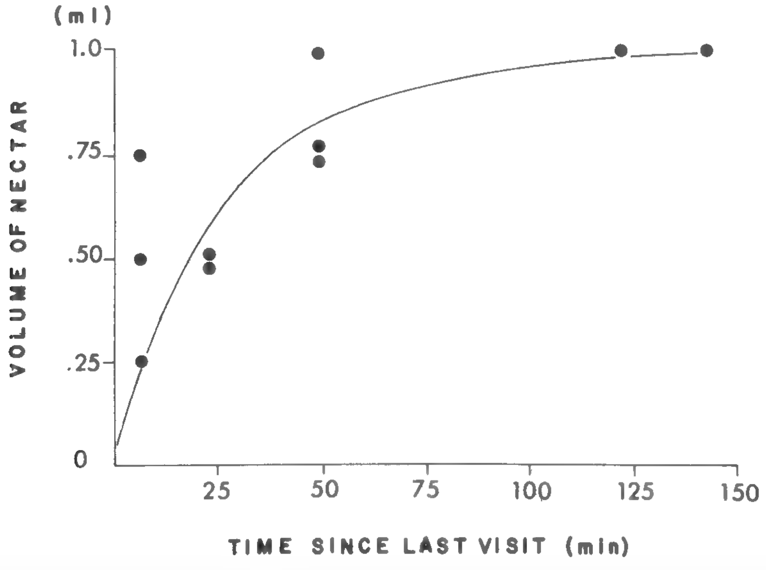

Figure 8. Rate of nectar production in *Exogonium bracteatum*. It takes about 55 minutes for an empty flower to produce about 85 percent of its maximal volume of nectar. Thereafter, further replenishment is very slow. Curve fitted by eye.

attracted only a small number of wanderers, mostly Violet-crowned Hummingbirds and Berylline Hummingbirds. *Ceiba* possesses few flowers per tree but each one produces a large amount of nectar toward the end of the day. Although it is exploited by bats, hummingbirds take as much nectar as they can before sundown. Since the daytime period for feeding on *Ceiba* is short, all individuals concentrate their efforts at feeding. Several species were seen visiting the same flower in sequence without conflict. Only when *Ceiba* is in bloom do Plain-capped Starthroats take more nectar than insects.

Lemairocereus produces open globular fruits covered with felt and brown bristles. The interior is filled with a red gelatinous substance exploited by several species of birds, including hummingbirds. Unlike the nectar of *Ceiba*, this gelatinous substance is available throughout the day and is nonrenewable. Therefore, as long as it is abundant enough to fill their daily energy requirements, Berylline Hummingbirds set up territories at each one of these cactus trees, and considerably reduce visits by other hummingbirds regardless of species.

Riparian Gallery Forest

During the dry summer only the two residents, Cinnamon Hummingbird and Fork-tailed Emerald, inhabit this forest, probably because they can balance their energy budget by making regular visits to gardens in the neighborhood. They are generalists in their feeding, consuming both insects and nectar. Nevertheless, their food niches overlap very little. Cinnamon Hummingbirds take nectar mostly from tubular flowers such as *Inga spuria, Caesalpinia pulcherrima*, and *Musa* sp., while Fork-tailed Emeralds concentrate on cup-shaped flowers like *Coffea arabica* and *Murraya paniculata*. Moreover, Cinnamon Hummingbirds defend feeding territories while Fork-tailed Emeralds trapline.

The number of flowers increases progressively from November onward. The resident species reduce their niche breadth, and intruders invade the habitat. Wanderers come first and are followed by migrants in December. When the latter arrive and are still uncommon, they feed either from cup-shaped flowers like *Calliandra* sp. (Broad-billed Hummingbirds), tubular flowers like *Psittacanthus calyculatus* (Violet-crowned and Berylline Hummingbirds), or insects (Plain-capped Starthroats, Ruby-throated Hummingbirds, and Black-chinned Hummingbirds). The residents maintain generalist diets which are well differentiated. In January, food becomes plentiful and specialization is maximal. Cinnamon Hummingbirds control the tubular flowers like *Psittacanthus calyculatus* and *Inga spuria*, while all the seasonal visitors join the other resident, the Fork-tailed Emerald, in exploiting the thousands of cup-shaped flowers of *Bumelia* sp. and *Paullinia sessiliflora*. While migrants and the majority of wanderers have feeding territories, the subordinate Emerald Hummingbird maintains its traplines and is the only species to visit the few flowers in *Russelia* sp. In February, the number of flowers dwindles and the seasonal visitors disappear gradually, leaving the two residents to their respective and well-segregated niches.

Arid Pine-Oak Forest

This is the most benign of the environments studied. Here the variations of air temperature and soil moisture are much smaller. At all times of the year seasonal visitors are present to feed on the array of flowering plants available to hummingbirds. The hummingbird species which make up the nectarivorous guild change regularly from season to season. Only the White-eared, Berylline, and Rivoli's Hummingbirds are present all year. Despite regular changes of species, the guild always includes some generalists and some specialists.

As in the two previous habitats, flowers are less common during summer than winter. Residents thus need to visit several types of flowers to fulfill their daily requirements of nectar, and are therefore more generalist than during winter. Moreover, Amethyst-throated Hummingbirds, which are aggressive wanderers, are common during summer and their territorial behavior monopolizes the best tubular flower of the habitat, *Malvaviscus arboreus*, thus forcing White-eared and Berylline Hummingbirds to visit several flower species of marginal suitability, mostly cup-shaped flowers. The former feeds mostly at *Fuchsia parviflora* while the latter prefers *Calliandra anomala*.

During winter, Amethyst-throated Hummingbirds become uncommon and Berylline Hummingbirds replace them at clumps of *Malvaviscus arboreus*. White-eared Hummingbirds maintain their generalist food niche, taking nectar from the majority of cup-shaped flowers, *Fuchsia parviflora* and *Phaseolus formosus* being preferred. Rivoli's Hummingbirds, which are rare during the summer, become more common with the blooming of *Cirsium anartiolepis* and *Lobelia laxiflora*. Finally, subordinate species such as wandering Broad-tailed Hummingbirds and migrant Calliope Hummingbirds are generalists that take advantage of the most abundant cup-shaped flowers. These are mostly *Lippia umbellata* and *Stachys coccinea* for the wanderer, and *Lagascea helianthifolia* and *Wigandia ureus* for the migrant. Moreover, Calliope Hummingbirds spent long periods of time feeding at an isolated clump of *Loeselia mexicana*, a very rewarding tubular flower neglected by dominant birds because of its isolation.

Humid Pine-Oak Forest

The daily variations of air temperature are great in this alpine habitat. During winter, and often during summer, the air temperature ranges from

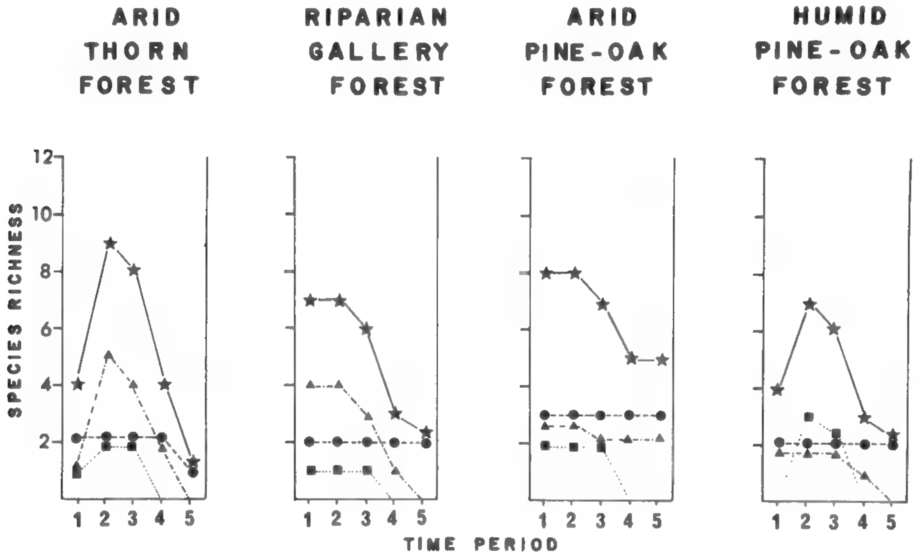

Figure 9. Total number of hummingbird species (★) and number of hummingbird species in each group (● = residents; ▲ = wanderers; ■ = migrants) found in the four habitats during the five time periods of the year: 1, arrival of migrants; 2, mid-winter; 3, departure of migrants; 4, end of the dry season; 5, beginning of the rainy season.

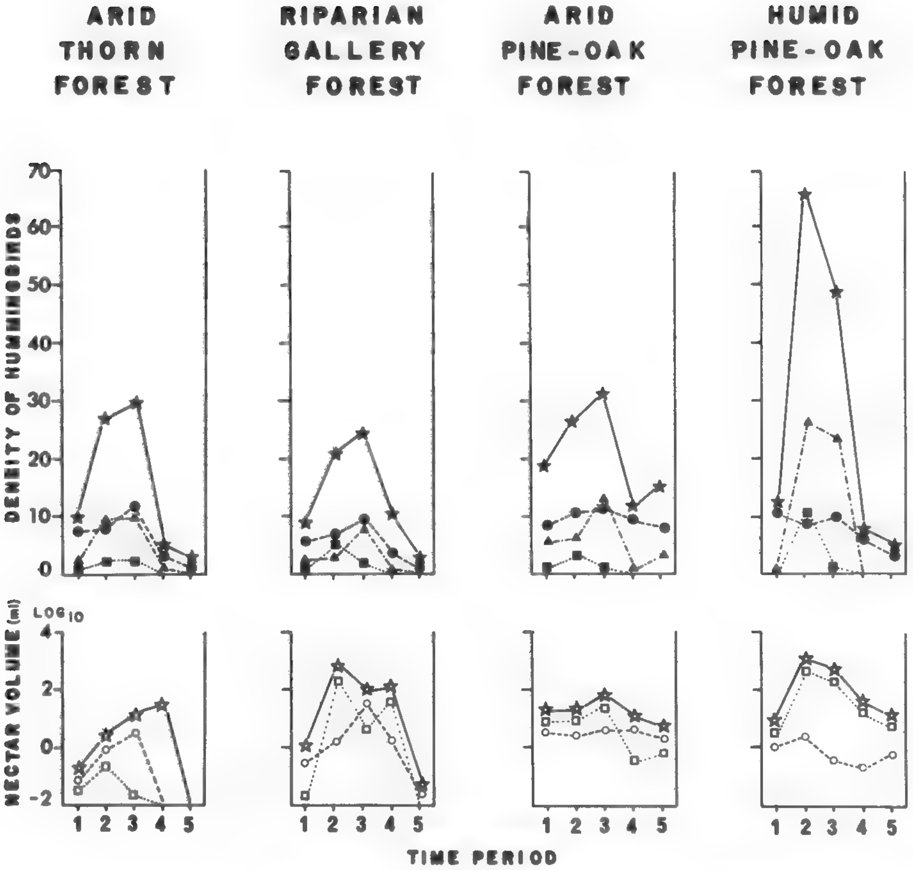

Figure 10. Total density of hummingbirds (★), number of individuals in each group (● = residents; ▲ = wanderers; ■ = migrants), $\log_{10}$ of the total volume of nectar in milliliters (☆), and $\log_{10}$ of volume in the two major types of flowers (○ = tubular flowers; □ = cup-shaped flowers) found in the four habitats during the five time periods of the year: 1, arrival of migrants; 2, mid-winter; 3, departure of migrants; 4, end of the dry season; 5, beginning of the rainy season.

the freezing point early in the morning to about 15°C around noon. Nevertheless, the few plant species adapted to this severe environment produce large numbers of flowers and attract several species of hummingbirds during the warmest period of the day. The hummingbirds spend the night at lower elevations, where the night temperature is milder.

There are two permanent residents in this habitat: the White-eared Hummingbird and Rivoli's Hummingbird. The first species is territorial and a generalist in its feeding, while the second is a trapliner and feeds mostly at *Cirsium* sp., although it also visits isolated clumps of flowers along its traplines, especially the tubular flowers of *Penstemon roseus*. The flowers most often used by White-eared Hummingbirds are *Penstemon roseus* and *Symphoricarpos microphyllus* during summer, and *Senecio angulifolius, Buddleia cordata*, and *Ribes ciliatum* during winter. Insects are also an important supplement to their diet.

As in the other habitats, flowers are very abundant during winter, which allows for the accommodation of several opportunistic seasonal visitors, in particular the Green Violet-ear and the Broad-tailed Hummingbird (wanderers), and the migratory Rufous Hummingbird. These hummingbirds concentrate their foraging at *Ribes ciliatum, Cestrum terminale, Buddleia cordata*, and *Senecio angulifolius*. They all have territories that they reestablish each morning, the best ones going to the aggressive Rufous Hummingbird.

Two active nests of White-eared Hummingbirds were found in February at a time when migrants were leaving this habitat. Nuptial chases of the two wanderer species were also regular at this time of the year, suggesting that they also breed at this time.

Organization of the Guild

Species Richness

The species of hummingbirds in each community varied seasonally, with the peak in the middle of winter (Figure 9). By definition, the number of resident species is always constant. However, the number of seasonal visitors in each community varies significantly. Migrants are present only during the winter. In the humid pine-oak forest, they constitute the group with the greatest number of species during this period of the year, while they represent the smallest cohort of species in the other habitats. Wanderers are also more numerous at the middle of the dry season. At this time they rejoin the majority of species living in the arid thorn forest and in the riparian gallery forest. They are almost as numerous as the residents in the two mountainous habitats.

Species Density

Correlation analyses presented in this section use data from all four habitats combined because sample sizes from individual habitats are too small. The total density of hummingbirds varied directly with species richness.[8] In all habitats, the number of hummingbirds fluctuates tremendously during the year (Figure 10). During the summer there are usually less than 15 individuals found along a one-kilometer transect, while during the winter there could be as many as 65 hummingbirds feeding along the same transect. However, the average maximum density is about 30 birds at this time. Fluctuations of abundance are the greatest in the humid pine-oak forest. The peak of maximum density occurs earliest (December) in this habitat.

Seasonal variations in density of hummingbirds are correlated with the seasonal changes in the abundance of nectar[9] (Figure 10). Fluctuations in the number of residents are concordant with the variations of nectar in both tubular and cup-shaped flowers,[10] while the changes of the numbers of wanderers and migrants parallel the variations of total volume of nectar in cup-shaped flowers.[11]

Species Diversity

The diversity (H′) of the communities varied seasonally. The minimum values occurred in summer, and the maximum values occurred in winter (Figure 11). Changes in diversity are correlated closely with its two components, species richness (Figure 9) and equitability (Figure 11). The former is the number of species in the sample, the latter the unevenness of species abundance. In a multiple regression analysis, species richness is responsible for 55 percent of the variation in diversity, while equitability explains an extra 34 percent. Density of wanderers contributes an additional 9 percent for a total of 98 percent of the variance explained.[12] Tramer (1969) found that changes in diversity of 267 breeding bird communities were correlated closely with species richness ($r = .97$), while the equitability component remained stable. He attributed this result to the fact that breeding birds occupy predictable environments, and maintain more or less even relative abundances through intraspecific territoriality. In contrast, these hummingbirds inhabit a relatively uncertain environment. The seasonal visitors are opportunistic species which are more or less abundant depending on the availability of food. Therefore, relative abundances vary significantly between species and seasons, and this variation has an important influence on the diversity of the communities.

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[8] d.f. = 18, $r = .52$, $p<.01$

[9] d.f. = 18, $r = .60$, $p<.01$

[10] d.f. = 18, $r = .67$, $p<.01$

[11] d.f. = 18, $r = .39$, $p<.05$

I used the total volume of nectar in each flower species to calculate season indexes of nectar diversity (Figure 11). Only residents responded to changes in nectar diversity. Their density is correlated with the diversity of nectar.[13] This suggests that residents behave as "equilibrium" species. They partition their environment according to the niches that are available. The more flower species and the more equitable the nectar distribution between them, the greater the number of viable niches and the greater the number of resident species, and thus individuals, that can coexist in the community. On the other hand, wanderers and migrants are opportunistic species which take advantage of seasonal surplus of nectar. Their numbers are affected solely by food abundance regardless of the ways in which the nectar surplus is divided among flower species.

Another possible reason why the diversity of the nectarivorous bird guild as a whole was not directly predictable on the basis of the nectar diversity might be the following. Most of the birds exploited many different plant species. This diet generalization partly buffers the effects on the birds of changes in the vegetation. Therefore, the generalist feeding strategy may represent an adaptation to the relatively short blooming periods of plants exploited by hummingbirds. Competition apparently has not been strong enough to eliminate the advantages of generalization despite the high interspecific overlap in diets, as has been suggested in the case of a herbivorous insect guild studied by Rathcke (1976).

Niche Breadth and Overlap

Niche breadth measures the degree of specialization of the niche of a species. Its value is large when several resources are used in equal proportions. The maximum possible value for niche breadth is 100. The mean niche breadth of the hummingbird species ranges from 26 to 91, although it usually lies between 75 and 85 (Figure 12). Therefore, the birds are rather generalist. Nevertheless, there is a tendency for niche breadth of all groups taken together (the relation is not significant when groups are taken alone) to decrease when the amount of nectar in cup-shaped flowers increases.[14] This reflects the more selective diet that is permissible when food is abundant (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971). No simple relations existed between niche breadth and the density of birds, their dominance, and the diversity of nectar.

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[12] d.f. = 18, multiple $r = .99$, $p<.01$

[13] d.f. = 18, $r = .57$, $p<.01$

[14] d.f. = 15, $r = -.47$, $p<.05$

Niche overlap measures the degree of similarity between the niches of a pair of species. It is large when the two species use similar resources in similar proportions. The maximum possible value for weighted niche overlap is 100. The mean overlap between the niches of our hummingbirds ranges from 0 to 41. Therefore, they occupy fairly distinctive niches. Although the majority of species feed from several of the flower species visited by other species, each one has a particular set of preferred flowers. This ecological segregation is often greater between species which belong to the same group, more specifically the residents (Figure 13). Conversely, migrants and wanderers more frequently overlap. Species that belong to the same group of birds probably exhibit less niche overlap because, being often in contact with each other, their niches have coevolved in order to be more rigidly complementary.

In a multiple regression analysis, seasonal availability of nectar is negatively correlated with overlap between residents' niches,[15] and is responsible for 38 percent of the variation in overlap, while hummingbird diversity (positive correlation) explained an extra 17 percent. On the other hand, the degree of overlap between wanderers' niches is negatively correlated with the density of residents.[16] No significant relation exists between the degree of overlap between niches of residents and wanderers and their respective seasonal density, or the seasonal availability and diversity of nectar.

Results of this analysis suggest that overlap between niches changes seasonally in a predictable way in relation to nectar changes. The paucity of food in some seasons forces residents to adopt more similar niches, while abundant nectar in relatively few flowers (thus low diversity) encourages wanderers to feed opportunistically from the same highly suitable flowers.

Finally, seasonal variations in niche overlap are positively correlated with changes in hummingbird diversity.[17] This is in agreement with the idea that

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[15] d.f. = 13, $r = -.59$, $p = .01$
[16] d.f. = 9, $r = -.77$, $p<.05$
[17] d.f. = 14, $r = .42$, $p = .05$

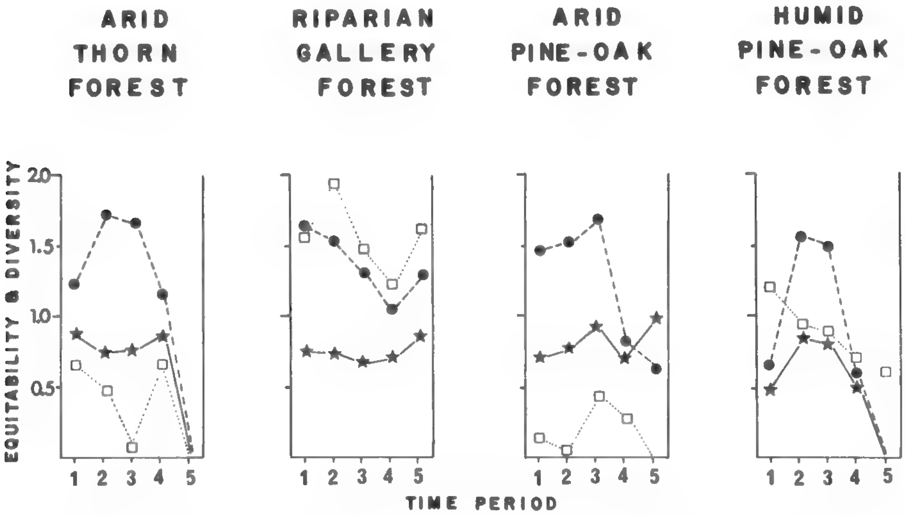

Figure 11. Equitability indexes of hummingbird communities (★), and Shannon indexes of diversity for hummingbirds (●) and flowers (□) found in the four habitats during the five time periods of the year: 1, arrival of migrants; 2, mid-winter; 3, departure of migrants; 4, end of the dry season; 5, beginning of the rainy season.

an increase in the similarity of coexisting species — stated differently, a reduction in the size of the exclusive portion of the species niche—can be a factor causing an increase in number of species (see Klopfer and MacArthur 1961). However, correlation can arise for another reason. When food is abundant, several species can enter the community without suffering intolerable competition, despite the fact that they forage opportunistically from the same flowers. Therefore, no causal relationships are inferred.

Partitioning the Food: Nectar

There are several ways in which bird species differ from each other in their use of available food. They can minimize competition by feeding on partially different foods, by taking foods at different heights or feeding sites, and by using different behaviors to find food. This section presents quantitative evidence of such segregation.

An analysis of nectar segregation between groups of hummingbirds is presented elsewhere (DesGranges and Grant, in press). I will summarize the major results. For each one of the three groups of birds (migrants, wanderers, and residents), I recorded feedings at tubular and cup-shaped flowers and analysed the data by multiple regression separately without making distinction for habitats and time periods. The few observations made at other types of flowers were insufficient for analysis. The use of a flower type (i.e., tubular or cup-shaped) by a species of bird in a habitat during a time period was the dependent variable. Independent variables included the relative availability of nectar, its suitability, its exploitation, the rank of the species in the dominance hierarchy, and its relative density in the guild. Appendix 1 provides definitions of these measures.

Residents are the principal users of tubular flowers. When they use them extensively, the exploitation of these flowers by wanderers and migrants is low.[18] Variation in the use of tubular flowers is principally attributable to resident species with a high dominance status. Conversely, the use of cup-shaped flowers by resident species is negatively related to their degree of dominance.[19] These results suggest that residents appropriate tubular flowers through aggressive interaction. Residents won most of their chases against the two other groups of birds at most flower species.[20] They dominate wanderers particularly at tubular flowers[21] and dominate migrants especially at cup-shaped flowers.[22]

Despite their competitive superiority in general, resident species which monopolize tubular flowers rarely modify their diet to feed at flowers with the most nectar. Relative availability of nectar in tubular flowers had only a moderate effect on the use of these flowers by the residents,[23] while the relative availability of cup-shaped flowers had no significant effect on the use of these flowers by the residents.[24] It appears that resident species preferen-

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[18] d.f. = 27, $r = -.49$, $p<.005$

[19] d.f. = 24, $r = -.57$, $p<.005$

[20] d.f. = 1, $X^2 = 12.0$, $p<.005$

[21] d.f. = 1, $X^2 = 3.8$, $p = .05$

[22] Binomial $p = .008$

[23] d.f. = 27, $r = .38$, $p<.05$

[24] d.f. = 24, $r = .05$, $p>.1$

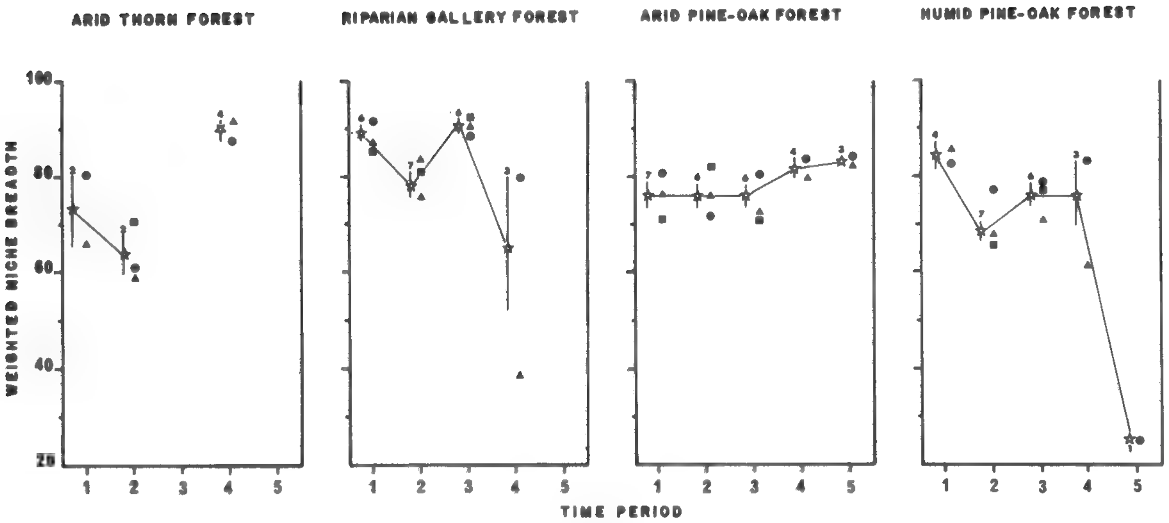

Figure 12. Mean values (Shannon absolute weighted niche breadth) for each group of hummingbirds in the four habitats during the five time periods of the year: 1, arrival of migrants; 2, mid-winter; 3, departure of migrants; 4, end of the dry season; 5, beginning of the rainy season. The mean value for the entire set of species (☆) is given with one $S\bar{x}$ on each side of the mean and sample size.

tially visit certain flowers, and they keep on feeding from them even if they are found together with flowers containing more nectar.

Wanderers are more sensitive than residents to variation in the relative availability of nectar in tubular flowers. When they are feeding at tubular flowers, wanderers feed more at flower species which contain a high proportion of the nectar available in the habitat and less at flowers which contain low nectar.[25] Since residents are the principal users of tubular flowers and have a high dominance status (see Plate 1), wanderers may be feeding on a nectar surplus which is not entirely controlled by residents in an aggressive fashion.

At cup-shaped flowers, the relative availability of nectar is responsible for only 18 percent of the variation in the use of cup-shaped flowers by wanderers, while seasonal density explains an extra 16 percent of the variation in a multiple regression analysis.[26] Their use of cup-shaped flowers, which are generally poorer energetically than tubular flowers, may be determined by aggressive interaction with residents at tubular flowers.

Migrants fed rarely at tubular flowers but foraged extensively at cup-shaped flowers. The use of these flowers by migrants is positively related to their relative availability.[27] In addition most data come from habitats and time periods when cup-shaped flowers were highly suitable. Thus migrants draw profit from the spectacular winter bloom of cup-shaped flowers (see Figure 7). For much of the time that migrants are present, this resource is abundant and competition with tropical species is weak.

Partitioning the Food: Arthropods

Most, if not all, hummingbird species supplement their diet with small arthropods they find in flower corollas, in the foliage of shrubs and trees, in the air (Feinsinger 1976; Wagner 1946; Wolf 1970; Young 1971) and occasionally on the ground (J.-L. DesGranges, pers. obser.; Vuilleumier 1969).

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[25] d.f. = 29, $r = .55$, $p<.005$

[26] d.f. = 23, $r = .42$, multiple $R^2 = .34$, $p<.05$

[27] d.f. = 10, $r = .51$, $p<.05$

In my study areas, this animal food usually consisted of small diptera. When flowers were abundant, most hummingbirds spent less than 20 percent of their feeding time foraging for small arthropods in comparison to almost 100 percent during periods when flowers were scarce, especially during the rainy season. The abundance of arthropods is higher in the late dry and early wet season than it is in the cool months of the dry season (Karr 1976). Certain species fed more extensively on arthropods than others. For example, Plain-capped Starthroats fed almost exclusively on aerial arthropods in all seasons except during the short blooming period of *Ceiba aesculifolia*, at which time nectar made up 96 percent of its diet. Amethyst-throated Hummingbirds also fed extensively on small arthropods. Only during the wet season when *Malvaviscus arboreus* was abundant did Amethyst-throated Hummingbirds feed largely on nectar.

Migrants and wanderers with a low dominance status also tended to take a greater proportion of arthropods than nectar, especially at their arrival and departure from a habitat. For example, *Archilochus* sp. spent almost 100 percent of its time feeding on arthropods when it arrived in the arid thorn forest and in the riparian gallery forest, and 61 percent of its foraging time just before its departure from the first habitat. The Lucifer Hummingbird, a subordinate wanderer, only ate arthropods at the time of its daily departure from the arid pine-oak forest.

Spatial Segregation of Hummingbirds

In order to test whether groups of species differed significantly in one or more niche dimensions, I used a subset of the original data consisting of those cases where species showed significant differences from all other species occurring with them temporally and spatially and using the same flower type. Comparisons involving all species in the different seasons and habitats were prohibitive due to the large number of combinations involved.

When several species of hummingbirds use the same food type, they may separate their ecological activities in several ways. Feeding activities may be confined to different parts of trees or bushes, such as the top and the bottom (Stiles and Wolf 1970), or the exterior and the interior of the vegetation (Colwell *et al.* 1974; Feinsinger 1976). In addition, species could select plants in different microthermal environments like sunny and shaded locations.

Study of the average height of feeding of coexisting species does not show any consistent pattern of spatial segregation between the different species. However, when we disregard taxonomic affiliations but pay attention solely to the behavioral characteristics of each individual, we find that dominant species and territorial individuals tend to feed at the tops of trees and shrubs, outside the vegetation, and at places where flowers are tightly packed together. On the other hand, subordinate species and non-territorial individuals feed often at the base of trees and shrubs (Fisher, $p = .11$), often inside the vegetation (Fisher, $p = .04$), and often at scattered flowers found at the periphery of the defended territories.[28]

In this manner, dominant species and territorial individuals can forage in a more efficient way, and they can exclude others. On the other hand, subordinate individuals escape from the vigilance of the previous individuals by visiting—silently and often sitting while feeding—the flowers situated in out-of-sight places.

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[28] d.f. = 3, $X^2 = 14.9$, $p<.05$

My data do not show segregation of species between microthermal environments. However, since there is a larger area of shade than sun, more feeding occurred in shaded places than in sunny ones. Nevertheless, hummingbirds were sensitive to this dimension of their environment. Early in the morning, hummingbirds of the cold humid pine-oak forest foraged preferentially in sunny locations. For example, before 07:30 hours, the White-eared Hummingbird spent 64 percent of its foraging time feeding in the few sunny spots along the transect while thousands of flowers located in the shade were underexploited. During the day in general, however, this species spent only 47 percent of its foraging time feeding in sunny locations.

Seasonal Segregation of Hummingbirds

Species which make up the guild of nectarivorous birds change regularly from season to season (Table 3). Residents are the only sedentary species, while wanderers and migrants visit the various habitats for short periods of time during the massive blooms of trees and shrubs. Thus there is a partitioning of resources along the seasonal dimension. This segregation lessens the intensity of competition between the numerous species of this specialized guild, and allows for a more efficient exploitation of resources which change asynchronously from month to month. In addition, the species of wanderers and migrants, and their respective densities, change regularly. In certain cases, there is a seasonal segregation between the wandering species of hummingbirds which temporarily visit a habitat. For example, the Amethyst-throated and the Bumblebee Hummingbirds were most abundant during the summer months in the arid pine-oak forest while the Blue-throated and Broad-tailed Hummingbirds were usually found there during the winter months. However, most seasonal visitors reached their maximum representation inside the communities during the winter peak of food abundance. They usually differed, though, in regard to their respective dates of arrival and departure from the various communities (see also

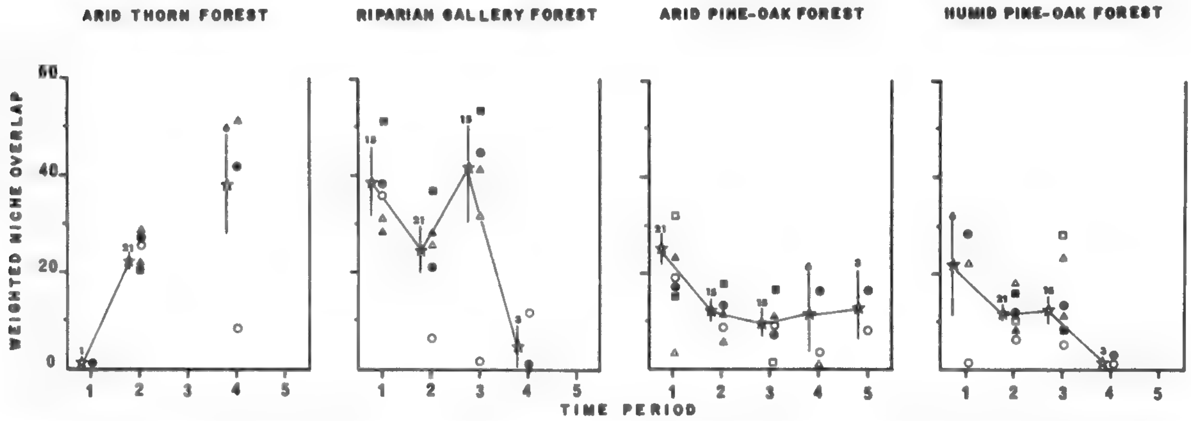

Figure 13. Mean values (Horn absolute weighted niche overlap, equation 23 in Colwell and Futuyma 1971) between groups of hummingbirds found in the four habitats during the five time periods of the year. The mean value for the entire set (☆) is given with one $S\bar{x}$ on each side of the mean and sample size. Symbols for species groups are as follows: ○ = residents and residents; Δ = wanderers and wanderers; □ = migrants and migrants; ● = residents and wanderers; ▲ = residents and migrants; ■ = wanderers and migrants. Time periods include: 1, arrival of migrants; 2, mid-winter; 3, departure of migrants; 4, end of the dry season; 5, beginning of the rainy season.

DesGranges 1977). For example, *Archilochus* sp. arrived in the middle of October in the arid thorn forest while Lucifer, Violet-crowned, and Rufous Hummingbirds appeared in early January. After the middle of February, Lucifer Hummingbirds were the only seasonal visitors still abundant in that habitat. In the riparian gallery forest, I first saw the majority of seasonal visitors at the end of October, but *Archilochus* sp. left around the middle of February, while Berylline and Broad-billed Hummingbirds remained there. Broad-tailed Hummingbirds came first in the humid pine-oak, around the last part of October, while Green Violet-ears and Rufous Hummingbirds were not common until the end of November. After the departure of the migrants, the wanderers stayed behind and probably nested.

Diurnal Segregation of Hummingbirds

Interspecific differences in the diurnal distribution of flower visits sometimes occur among bees (Linsley *et al.* 1963) and hummingbirds (Feinsinger 1976). Besides the Green Violet-ear, which was much more active than any other species of hummingbird at the end of the day (60 percent of its foraging time occurred after 17:00 hours), my data do not show any clear-cut cases of diurnal segregation between the species I studied. However, I noted a trend for the most dominant species (i.e., most residents and wanderers) to start their feeding early in the morning, to slow down during the middle of the day, and to start again in late afternoon. On the other hand, subordinate species (i.e., most migrants) tended to feed mostly from the middle of the morning to the middle of the afternoon.[29] It is possible that dominant species aggressively limit visits of other species during the periods of the day when nectar is most abundant in flowers, especially the morning, but I did not measure this. However, since nectar is usually abundant when subordinate species visit the communities, I think that great divergence among diurnal foraging patterns would be superfluous. I am inclined to attribute the partial segregation I observed to the fact that the larger dominant birds[30] can feed during periods of the day when the air temperature is too low for the smaller subordinate species to forage efficiently.

Sexual Segregation of Hummingbirds

It is theoretically possible to distinguish in the field the sex of 15 of the 21 species of hummingbirds under study (Peterson and Chalif 1973; Robbins *et al.* 1966); see Table 2. However, immatures of the sexually dimorphic and dichromatic species have a plumage which often closely resembles that of the adult females. Therefore, I will treat immatures and females as a single group in the present analysis.

In the majority of the sexually dimorphic species, both sexes share a common niche. However, two species exhibited a noticeable degree of intersexual segregation. In the Fork-tailed Emerald, males foraged preferentially for nectar in cup-shaped flowers such as *Murraya paniculata, Coffea arabica, Bumelia* sp., and *Paullinia sessiliflora* (75% of visits). Females and immatures foraged more regularly for insects (48% of feedings), and less often for nectar (52% of visits), mainly in rare cup-shaped flowers such as *Russelia* sp.

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[29] d.f. = 3, $X^2 = 9.0$, $p<.05$

[30] Canonical $r = .93$, $p = .003$

and *Quamoclit hederaefolia*. A similar pattern of sexual segregation prevails in the Puerto Rican Emerald, *Chlorostilbon mangaeus*, with males foraging primarily for nectar (67% of feedings), and females taking mostly insects (74% of feedings; Cameron Kepler, pers. commun.). However, in this case, females forage mainly under vegetative cover, while I found no such intersexual difference in my species. In the White-eared Hummingbird, adult males aggressively excluded females and immatures from the most suitable clumps of flowers and thereby forced them to take nectar in flowers found under vegetative cover, such as *Stachys coccinea* and *Fuchsia microphylla*. These two cup-shaped flowers were the only flower species out of the 25 used by the White-eared Hummingbird at which females and immatures fed more often than males—93% of the feeding events at the two flower species combined. Moreover, insects were more important in the diet of females and immatures (23% of feedings) than in the diet of males (15% of feedings).

Selander (1966) suggests that species of birds which form pairs holding feeding and nesting territories commonly alleviate intersexual competition by moderate niche differentiation. The White-eared and Emerald do not show this. Instead, males have a broad niche while females are specialized within the range of the niche of the other sex.

Competition with other Nectarivorous Animals

Besides hummingbirds there are several other groups of birds and animals which exploit the nectar of flowers. Fisk and Steen (1976) present a table of thirty-three North American bird species, other than hummingbirds, which are known to feed on nectar. Hummingbirds (Trochilidae), honeycreepers and flower-piercers (Coerebidae), orioles and caciques (Icteridae), and finches (Fringillidae) are the families which contribute the greatest number of nectar feeders. My study adds four additional exploiters of nectar. They are the Ruby-crowned Kinglet *(Regulus calendula)* in the Sylviidae, and the Orange-crowned Warbler *(Vermivora celata)*, the Nashville Warbler *(V. ruficapilla)*, and the Tropical Parula *(Parula pitiayumi)* in the Parulidae. Moreover, the Orange-breasted Bunting *(Passerina leclancherii,* Fringillidae) often fed from the sweet flesh of *Lemairocereus* fruits in company with hummingbirds.

Bats and several types of insects such as bees, wasps, butterflies, moths, beetles, ants, and dung flies also exploit the nectar and/or the pollen of flowers. However, these species ordinarily visit flowers which have coevolved with their pollinators and have a particular morphology which facilitates the exploitation of nectar by the symbiotic species and prevents visitation by other species (van der Pijl 1961). Therefore, hummingbirds and other animals are rarely competing with each other since they exploit the nectar of different classes of flowers pollinated by animals. Not a single aggressive interaction was noted between a hummingbird and an insect. This suggests that either insects are taking pollen when they are feeding at flowers used by hummingbirds, or the nectar is so abundant that competition is non-existent.

However, on rare occasions a hummingbird tried to exclude another bird from its territory. Most chases were directed against warblers, flower-piercers, and kinglets, but on a few occasions groups of hummingbirds attacked larger birds which were non-nectar feeders. Species which were "mobbed" included the Ferruginous Pygmy-owl *(Glaucidium brasilianum)*, the American Kestrel *(Falco sparverius)*, the Rough-winged Swallow *(Stel-*

gidopteryx ruficollis), and several passerine species which form flocks of feeding birds.

Warblers and kinglets are predominantly insect-eaters. When feeding on nectar, they move continuously from one clump of flowers to another, spending a relatively short time at each one. Therefore, it is probable that the quantity of nectar they rob in each hummingbird territory is negligible. This could explain why interactions between them and hummingbirds were so infrequent. The Cinnamon Flower-piercer *(Diglossa baritula)* was common in the arid pine-oak forest during the summer. It is an insectivorous species which supplements its diet with nectar. At the beginning of the rainy season, it spent 49 percent of its foraging time eating nectar. However, each time it was seen feeding on nectar, it fed concealed in the vegetation. Therefore, competition with hummingbirds would be minimal since hummingbirds concentrate their foraging on flowers in the outer parts of shrubs. A similar pattern of spatial segregation exists in the Slaty Flower-piercer, *Diglossa plumbea* (Colwell *et al*. 1974)

Discussion

I am critically aware of the limitations of the "coarse-grained" approach I have adopted for this study. In grouping flowers, birds, and days into conspicuous clusters, I sought to emphasize the major ecological relationships between residents, wanderers, and migrants, and hoped that the detailed information lost in the process would not have contributed much to a complete understanding of the organization of this tropical bird guild.

Another shortcoming of my analysis is that I only considered linear relationships and ignored possible non-linear and threshold relationships. Inspection of the data shows this restriction to be reasonable. Although my study was observational rather than experimental, I assumed that correlations noted between ecological variables are probably attributable to cause and effect relationships. This assumption needs to be tested experimentally.

In the following discussion, I will use (1) my quantitative data, (2) unquantitative observations, and (3) information from the literature, to outline the major ways in which hummingbird communities in the tropics are organized.

The number of hummingbird species and their density in the habitats varied seasonally, with peaks in the dry season, the major flowering season of the year. Bird species that face seasonal irregularity in the availability of food resources may (1) shift to feeding on other resources or they may (2) move to another area where the original food resource is available. Seasonal regularity in food supply does not necessitate (3) movement or diet shift. These three general behaviors were observed to variable degrees in the nectarivorous bird guild I studied. The guild is made up of nomadic species which are either unique specialists on uniquely shaped or exceptionally long flowers (e.g., Long-tailed Hermit) or opportunistic generalists, such as the majority of wanderers and migrants, superimposed on an assemblage of sedentary species. The latter are either specialists such as Plain-capped Starthroat and Rivoli's Hummingbird, generalists such as Fork-tailed Emerald and White-eared Hummingbird, or according to the seasonal abundance of food, both, such as the Broad-billed, Cinnamon, and Berylline Hummingbirds. The last group occasionally acts as nomadic species in neighboring communities.

The nectarivorous bird guild responds readily to changes in food abundance. In general, residents have a high status of dominance in interspecific interactions. They form the core of the guild to which additional species are added, depending on the seasonal availability of food. Most resident species feed preferentially on tubular flowers and prevent other hummingbirds from feeding from them by threatening or attacking them. Nevertheless, some species, particularly the subordinate ones, feed mostly on cup-shaped flowers. Tropical wanderers usually are trapliners and have a high status of dominance. They are sequential generalists feeding on tubular and cup-shaped flowers that cannot be exploited by the residents. Migrants are small birds and thus tend to be subordinate to residents and wanderers. They are territorial and use abundant, and/or sporadically available, flowers, mostly cup-shaped, that exceed the requirements of the residents and wanderers (see also DesGranges and Grant, in press). Most of these flowers are small and produce small quantities of nectar, making them efficiently exploitable by small birds with low total energy requirements. When flowers are rare and/or entirely defended by superior competitors, insects are an important supplement to the migrants' diet.

No species has a bill that gives it exclusive access to flowers of a particular species. The exception is the Long-tailed Hermit, which has a long bill, and was the only hummingbird species able to feed at flowers of *Lindenia rivalis*. This suggests that guild members maintain food segregation by competition more than by coevolution between particular flowers and birds, as is the case with the hummingbirds studied by Snow and Snow (1972) and Stiles (1972). Size of the birds determined interspecific dominance[31] and was also the major determinant of flower patch selection (see Stiles and Wolf 1970; Wolf 1970; Wolf *et al.* 1976). Size is responsible for the partial segregation of species along the food axis, with the residents feeding preferentially at tubular flowers and migrants foraging mostly at cup-shaped flowers. However, I found no species that used a major flower species exclusively. This is attributable to the highly developed exploratory behavior of the hummingbirds studied. It may be advantageous for hummingbirds to sample a variety of different flowers in different areas, often in defended territories, before becoming at least temporarily site- and flower-specific, especially if territories then could be set up around suitable clumps of flowers (see Heinrich 1976).

In general, as the stability of food resource increases, the diversity of the fauna exploiting that resource increases (Karr 1976; Slobodkin and Sanders 1969). However, in the guild I studied, diversity is high despite seasonal irregularity in nectar availability. The species are apparently limited by food, and the seasonal variations in the availability of their principal food, nectar, are strong but apparently predictable. It seems that severe food limitation allows few species to coexist between major flowering seasons. Therefore, unused food becomes available during periods of extensive blooming. The resident populations are unable to consume all the food locally produced, because the low carrying capacity of their environment during other periods of the year keeps their populations low. Predictable variation allows opportunistic species living in foreign communities to invade the habitat periodically, so that diversity increases.

Tropical species in general are packed tightly along habitat gradients

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[31] c.f. = 19, $r = .76$, $p<.01$

(Janzen 1967b). This partly explains the high diversity of tropical communities (MacArthur 1969). Habitats in Colima are varied and each one possesses a particular set of species which can migrate to other habitats when the residents there fail to use all the available food. Central America also possesses a great diversity of food sources (Karr 1967), and many birds, especially hummingbirds, migrate seasonally between habitats (Colwell 1973; Feinsinger 1976; Skutch 1967; Slud 1964; Wagner 1946; Wolf 1969; Wolf *et al.* 1976). The existence of such nomadic species is obviously a major reason for the high diversity of communities living in tropical regions. Where nomadic migrations are fewer, diversity is also limited. For example, Willis (1974) ascribes decreasing diversity in the Barro Colorado Island avifauna to the water barrier which inhibits migration across it. Similarly, Feinsinger (1976) explains why each small, homogeneous Caribbean island supports only two hummingbird species, one large and one small; to exploit seasonal flushes of food, wanderers would have to migrate between islands or between island and mainland, and the cost of such migration might outweigh the benefits.

I found that hummingbirds exploited fewer species of flowers in seasons of greater nectar availability and fed at a greater variety of flowers when the amount of nectar was less.[32] Several authors have suggested that animals should be more selective in their choice of food items when food is common, and more indiscriminate when food is scarce (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971). The basic argument is that the variety of food taken will expand as long as the resulting gain in time and/or energy spent per item or unit of food exceeds the loss (MacArthur and Pianka 1966). It appears that hummingbirds are more specialized in their feeding when abundant flowers are distributed in large monospecific clumps than when flowers are scarce and distributed in small clumps of one or many species. It is safe to say that data from this analysis of niche breadth are in accord with the classical theory of feeding strategies (Schoener 1971).

Overlap of niches also changed seasonally in relation to nectar changes. Residents had more similar diets when nectar was rare,[33] while wanderers foraged in a more similar fashion when large quantities of nectar were concentrated in few flowers.[34] It appears that residents feed mostly at flowers of their own particular niche when food is abundant, while they feed more often at flowers that belong to other resident species' niches when food is rare. Hence overlap between resident species is greater when food is scarce. On the other hand, wanderers behave like opportunistic species. They take advantage of food flushes. Since most species select the same abundant flowers, overlap between diets of several species increases when large nectar supplies are concentrated in few flower species. Future work should be directed toward identifying the causal factors that are responsible for the maintenance of these two opposite strategies of accommodation in the community.

According to Wolf *et al.* (1976), the tropical highland hummingbird community they studied in Costa Rica was in a state of early succession (as defined in McNaughton and Wolf 1970) with few species manifesting strong dominance. They attributed this to an aggressive resident, the Fierythroated Hummingbird *(Panterpe insignis)*, the guild organizer. Through its generalist feeding habit, it kept away resident specialists. The four communities I studied seem to be in a more advanced stage of succession. Diversity was relatively high, with a large number of species and a relatively even distribution of individuals between species, especially during the dry season. In addition, in three habitats, the guild included a resident specialist (Plain-capped Starthroat or Rivoli's Hummingbird) while in the fourth habitat the guild included a wanderer which is a specialist in its feeding (Long-tailed Hermit).

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[32] d.f. = 15, $r = -.47$, $p < .05$

[33] d.f. = 13, $r = -.59$, $p = .01$

[34] d.f. = 9, $r = -.67$, $p < .05$

Finally, the presence of both territorial and traplining species is an important aspect of the high diversity of tropical nectarivorous bird guilds. The existence of these two complementary foraging specializations results in the stable coexistence of closely similar species since it allows for a finer division of resources: territorial species exploiting clumps of flowers and trapliners feeding at scattered flowers.

Summary

This paper explores how nectar availability and interspecific competition influence flower visitation and the seasonal occurrence of the different hummingbird species. Eight months' observations on hummingbird foraging patterns in four habitats of the State of Colima in Mexico provided evidence that the guild of hummingbirds changes in response to food abundance.

The guild is composed of three groups of hummingbirds. A first group comprises the residents. They are tropical species which inhabit particular habitats even when the amount of flowers dwindles. A second group is made up of wanderers. They nest in tropical regions but, unlike residents, they are not present all year in a particular habitat. Instead, they visit several habitats during the year, following seasonal blooms of trees and shrubs. Finally, migrants form a third group. These species breed in the north temperate regions during the summer and invade the tropical regions during winter.

In general, residents show a high degree of dominance in interspecific interactions. They form the core of the guild to which additional species are added, depending on the seasonal availability of food. Most resident species feed preferentially on tubular flowers and often are territorial around clumps of these typical hummingbird flowers. Nevertheless, some resident species are "trapliners" and others, particularly the subordinate species, feed mostly on cup-shaped flowers. Tropical wanderers usually are trapliners and have a high degree of dominance. They are sequential generalists who feed on tubular and cup-shaped flowers which cannot be exploited by the residents. Migrants are small birds and tend to be subordinate to residents and wanderers. They are terrritorial and use abundant and/or sporadically available flowers, mostly cup-shaped flowers which provide nectar in excess of the residents' and wanderers' requirements. Insects are an important supplement to their diet.

Hummingbirds had a more restricted diet in seasons of greater nectar availability and a more diversified diet when the amount of nectar was less. Overlap between niches also changed seasonally in relation to nectar changes. Residents had a more similar diet when nectar was rare, while wanderers foraged in a more similar fashion when larger quantities of nectar were concentrated in fewer flowers.

Hummingbird communities appeared to be in a relatively advanced stage of succession. Diversity is relatively high. Communities comprise territorial and traplining species, as well as sedentary and nomadic species. These species are either unique specialists, feeding on uniquely shaped or exceptionally long flowers; opportunistic generalists; or both, according to the seasonal abundance of food.

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Appendix 1

Terms used in analyses

Term	*Definition or equation*
Indices	i = a hummingbird population (i = 1 to m) j = a flower type (j = 1 to n) h = a habitat (h = 1 to 4) t = a time period (t = 1 to 5)
Availability of nectar	A_{jht} = total amount of nectar (in ml) in a flower type at mid-day, in a habitat, during a period of the year.
Relative availability	$RA_{jht} = (A_{jht} / \sum_{j=1}^{n} A_{jht}) \times 100$
Foraging time	F_{ijht} = total amount of time that a hummingbird population has spent feeding at a flower type, in a habitat, during a period of the year.
Utilization of a food type	$U_{ijht} = F_{ijht} / \sum_{j=1}^{n} F_{ijht}) \times 100$
Exploitation of a food type	$E_{ijht} = (F_{ijht} / \sum_{i=1}^{m} F_{ijht}) \times 100$
Index of dominance	ID_i = 1 to 5 depending on the place of the species in a hierarchy of dominance in interspecific interactions (see text).
Density of hummingbird population	D_{iht} = average number of individuals of a certain hummingbird population which are seen during the visit to a habitat, at a particular period of the year.
Relative density	$RD_{iht} = (D_{iht} / \sum_{i=1}^{m} D_{iht}) \times 100$

After DesGranges and Grant, in press.

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A NESTING STUDY OF THE BROWN CREEPER

CHEYLEEN M. DAVIS

The Brown Creeper *(Certhia familiaris)* is a small passerine in the family Certhiidae. Its range covers the forested regions of North America and Eurasia.

World-wide, there are only five other members of this family, all in genus *Certhia* and found on the Eurasian continent.

In North America the Brown Creeper is the only member of the family Certhiidae. Although it feeds on arthropods found on the bark of trees, it does so in a different manner than other bark-foraging species. Nuthatches (Sittidae) and woodpeckers (Picidae) usually disturb the bark in their efforts to dislodge food material and nest in natural cavities or in holes that they excavate themselves. The Brown Creeper does not disturb the bark as it uses its long (15 millimeter), slightly decurved bill to pick food items from cracks and crevices and off the bark surface. Almost always, it nests between the bark and trunk of a dead or dying tree, where the bark has pulled away from the tree.

In this study, I observed and described the Brown Creeper's nesting cycle as it related to its feeding habits.

Study Areas and Methods

Time spent at Reese's Bog and Neithercut Woodland spanned nesting periods from June 1971 through July 1973. The study involved 345 hours of field observations made over 119 days. Of the total field time, 112 hours over 55 days were spent at Reese's Bog during the summers of 1971 and 1972. A more concerted effort was expended at Neithercut Woodland in 1973, when 233 hours were spent over 64 days from 5 April to 28 July.

In order to observe the Brown Creepers in relation to the entire habitat, I used no blinds. The birds continued their activities in and out of the vicinity of the nests while under observation from a distance of 3 to 6 meters.

I marked eggs in nests with small dots of colored tempera paint for identification.

Since adult male and female Brown Creepers are similar in size and coloration, sex identification was based on the fact that only the males sang. Individual recognition was based on size, feather coloration, and habits.

Observations centered around 20 Brown Creeper nests found during various phases of the birds' nesting cycle: Nests N1–N5 in Reese's Bog, 1971; Nests N6–N8 in Reese's Bog, 1972; and Nests N9–N20 in Neithercut Woodland, 1973. All nests contained at least one egg or young except Nest N9 which was abandoned after two days of nest construction because of human disturbance at the site.

I observed most of an entire nesting cycle at Neithercut Woodland. Observations began on 5 April 1973, two months earlier than observations in other years at Reese's Bog. Prenesting activities included territory establishment, courtship, and cavity searching. Nest building began on 21 April. Seven nests contained eggs by 1 June and four nests contained young by 7 June (Figure 1). Although all young fledged by 14 July, I recorded family groups from 6 June to 21 July.

The study areas were in Michigan's Lower Peninsula and included an area of Reese's Bog approximately 22 hectares in size (Figure 2) at the north end of Burt Lake, and a section of Neithercut Woodland (Figure 3) of about 78 ha in Clare County. They represented two differing environments where Brown Creepers nest.

Reese's Bog is an old white cedar *(Thuja occidentalis)* swamp. Major tree species included white cedar, balsam fir *(Abies balsamea)*, and black spruce *(Picea mariana)*. Here also were smaller numbers of large-toothed aspen *(Populus grandidentata)*, sugar maple *(Acer saccharus)*, red maple *(Acer rubrum)*, white pine *(Pinus strobus)*, basswood *(Tilia americana)*, and paper birch *(Betula papyrifera)*. Where the trees were thick, hindering sunlight from reaching the forest floor, undergrowth such as wintergreen *(Gaultheria procumbens)*, wild strawberry *(Fragaria virginiana)*, and slender red maple seedlings were thinly scattered. This vegetation grew in and through various levels of a tangled mass of dead limbs and tree trunks. Where water drainage held back tree growth and allowed more sunlight to reach ground level, both herbaceous and woody plant species were more abundant. Dense sphagnum moss *(Sphagnum centrale)* carpeted the banks of the small streams. In this sphagnum grew twin-flowers *(Linnaea borealis)*, wild lily-of-the-valley *(Maianthemum canadense)*, bead lilies *(Clintonia borealis)*, bishop's cap *(Mitella nuda)*, and starflowers *(Trientalis borealis)*. There was a denser covering of sphagnum in the numerous, small, open, park-like areas where the water was cut off from the streams. Here there were wood lilies *(Lilium philadelphicum)* and showy lady's slippers *(Cypripedium reginae)*. Young balsam fir filled some of the dryer forest openings, while wetter areas supported shrubs such as Labrador tea *(Ledum groenlandicum)*. Poison ivy *(Rhus radicans)* seemed to grow everywhere.

Neithercut Woodland is markedly different from Reese's Bog, presenting a wider variety of soil types, water drainage patterns, and floral species. On the dry, poor, sandy uplands there were mainly grasses and forbs interspersed with patches of blackberries (*Rubus* sp.), raspberries (*Rubus* sp.), and an occasional white oak *(Quercus alba)*, red maple, or American elm *(Ulmus americana)*. Where the soil was well drained, but moist and rich from humus deposits, there were mixed tree stands where red maple and American beech *(Fagus grandifolia)* predominated. The less numerous tree species here included eastern hemlock *(Tsuga canadensis)*, large-toothed aspen,

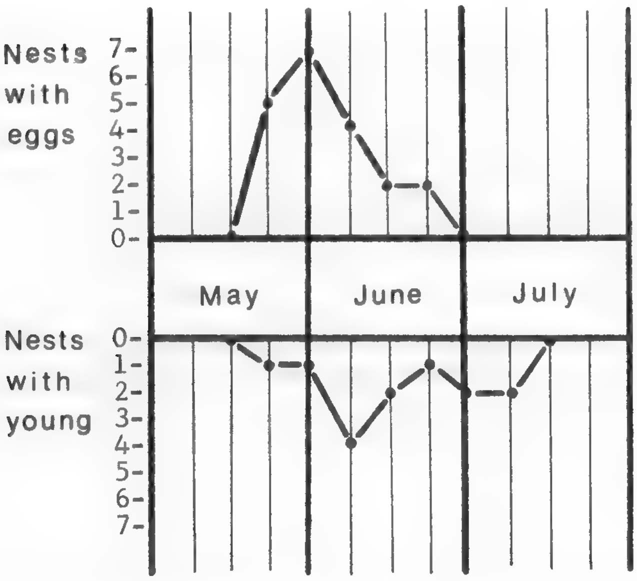

Figure 1. The timing of nests with eggs and young at Neithercut Woodland.

American elm, and bitternut hickory *(Carya cordiformis)*. Often barely above the leaf litter covering the forest floor were seedlings of red maple, American beech, and eastern hemlock, as well as herbaceous flowering plants such as round-lobed hepatica *(Hepatica americana)*, spring-beauty *(Claytonia virginica)*, and adder's tongue *(Erythronium americanum)*. In contrast, around and in small poorly-drained pockets that formed vernal and autumnal ponds, as well as along the stream courses, the forest changed to the prominent remains of American elm. Killed by the fungus *(Ceratocystis ulmi)* associated with the Dutch elm disease, there remained only weakened trunks and branches susceptible to wind and precipitation. Even here there were scattered red maple seedlings among the red osier dogwood *(Cornus stolonifera)*, alder (*Alnus* sp.), gooseberry (*Ribes* sp.) brush, and tangled growth of slender nettles *(Urtica gracilis)*, growing as ground cover in full sunlight afforded them when the elms lost their foliage. More dead elm (and dead basswood) filled three one-to-three ha tracts on the Neithercut property. These were situated behind old, abandoned beaver dams and probably died from inundation, rather than from infection. Living basswood still dotted the edges of these wet areas, along with occasional yellow birch *(Betula alleghaniensis)* and paper birch. Where the edges got wetter and the soil got sweeter, there were dense stands of white cedar and eastern hemlock. Undergrowth was sparse.

Territoriality

Territorial singing occurred commonly at Neithercut in April, May, and early June. By then eight (possibly nine) males and their mates had nests containing eggs or young. Singing continued until the young fledged, after which I heard few Brown Creeper songs.

The high-pitched notes composing the song of the Brown Creeper were audible up to about 120 meters away in mixed deciduous woods. Only one Brown Creeper was distinctly recognizable by his song.

In establishing their breeding territories, males often sang from vertical perches in the tops of trees that varied from dense cedar to the barkless remains of dead American elm 15 to 20 meters in height (Figure 4). Each bird usually remained stationary and sang one to eight songs per minute and up to four songs per perch. Then the bird flew to another branch on the same tree, to another tree perhaps 10 to 20 meters away, or from one forested area to another following an undulating, tree-top-level flight path across the opening. Singing periods occurred sporadically throughout the daylight hours from as early as 04:50 to 19:17 hours and lasted from 1 to 22 minutes.

As far as I could determine, creepers rarely sang from these distinct perches after territory establishment. Males stopped briefly to sing on lower tree trunks as they searched for food. Regardless of position, however, males establishing or maintaining territories often answered other males in adjacent territories during singing periods.

Singing rates were directly proportional to the amount of observed intraspecific territorial competition in the nesting areas at both Neithercut and Reese's Bog. No noticeable competition occurred in the vicinity of Nest N2. Thus, during one all-day study conducted from 04:52 to 20:12 hours on 15 June 1971 (three days prior to fledging), the adult male sang only 11 songs as he fed nestlings. At the opposite extreme, males from Nests N11, N12, N16, N17, and N19 (Neithercut) gathered where their established territories loosely adjoined and sang a total of 88 songs (Figure 5) in one hour on 5 June 1973.

The stage of the breeding cycle varied. One female had just finished building her nest (N19); another (N17) was laying eggs; one female was incubating (N11); young were hatching at Nest N12; and Nest N16 contained fourteen-day-old nestlings.

Males establishing territories displayed even greater song rates, the most extreme case occurring on 14 April as two males in the vicinity of N17 sang back and forth 53 times in less than ten minutes.

I determined approximate outlines of territories at Neithercut (Figure 6) from singing positions, nest locations, and known feeding areas for

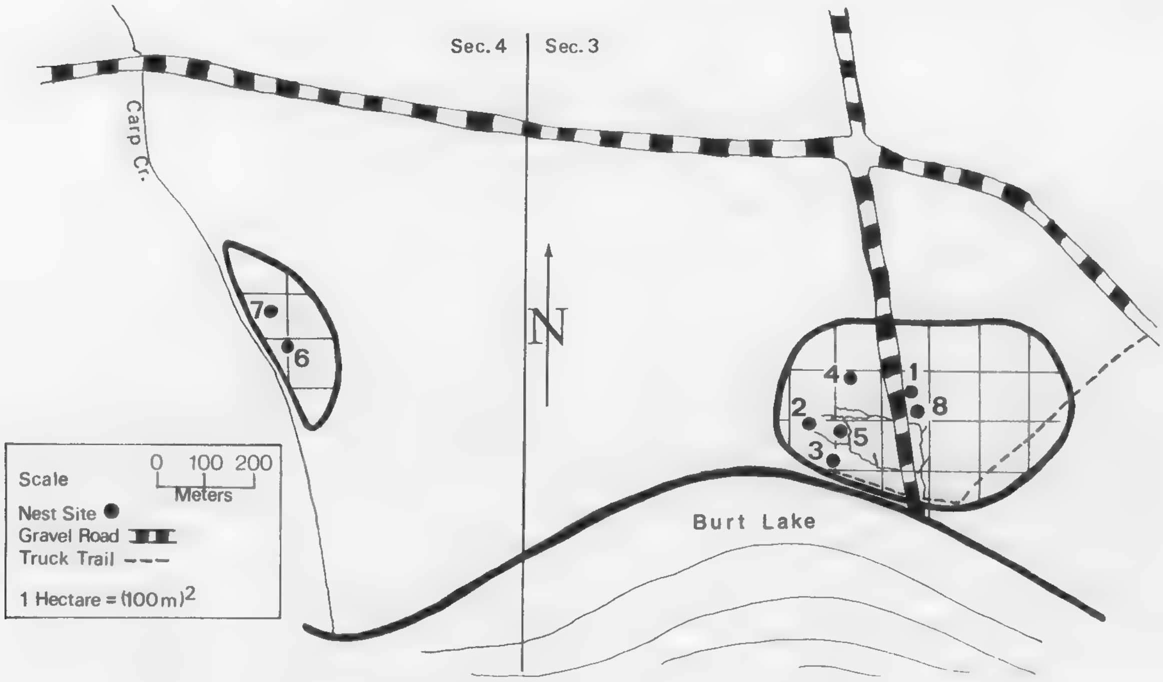

Figure 2. The study area in Reese's Bog, Cheboygan County, Michigan in 1971 and 1972.

individual pairs. There were seven known territories where nesting activities took place. There were three suspected territories. Distinct pairs of creepers inhabited suspected Territories A and B, but no active nests were found. I was unable to determine the boundary for N13, since the pair deserted and could not be found. Multiple nestings resulted from renesting attempts following nesting failures. In no case did a pair attempt to renest after successfully fledging their brood.

Territory size ranged from 2.3 to 6.4 ha. Birds holding smaller territories engaged in more vocal defense than those with larger territories.

Dement'ev *et al.* (1954) stated that Brown Creepers in Europe often fight in defending their territories. During my study I recorded no physical contact between male creepers. In fact, I saw a possible threatening display only once, and this involved an interaction with another species. On 4 April the N11 male was singing near the top of a dead American elm when a flock of Golden-crowned Kinglets *(Regulus satrapa)* flew into a cluster of white cedar near the creeper's singing position. The Brown Creeper stopped singing as the kinglets called to one another and then silently dropped towards a kinglet with a fast, bat-like series of spirals, such that I saw the white of his belly before he landed head up on a tree trunk. Then he flicked his wings several times and spiraled at another kinglet. Both kinglets that attracted his attention ignored him and kept moving with the flock as the Brown Creeper followed. The kinglets' call notes were very similar to the Brown Creeper's which may have resulted in the creeper's response.

Pair-bond Formation and Maintenance

The Brown Creepers' courtship activities include display flights, courtship chases, wing fluttering, and courtship feeding. Bent (1964) describes the display flights as short series of darts and twists around tree trunks. During such activity the birds' white underparts are conspicuous. In courtship chases the male closely pursues the female as they spiral up and down the

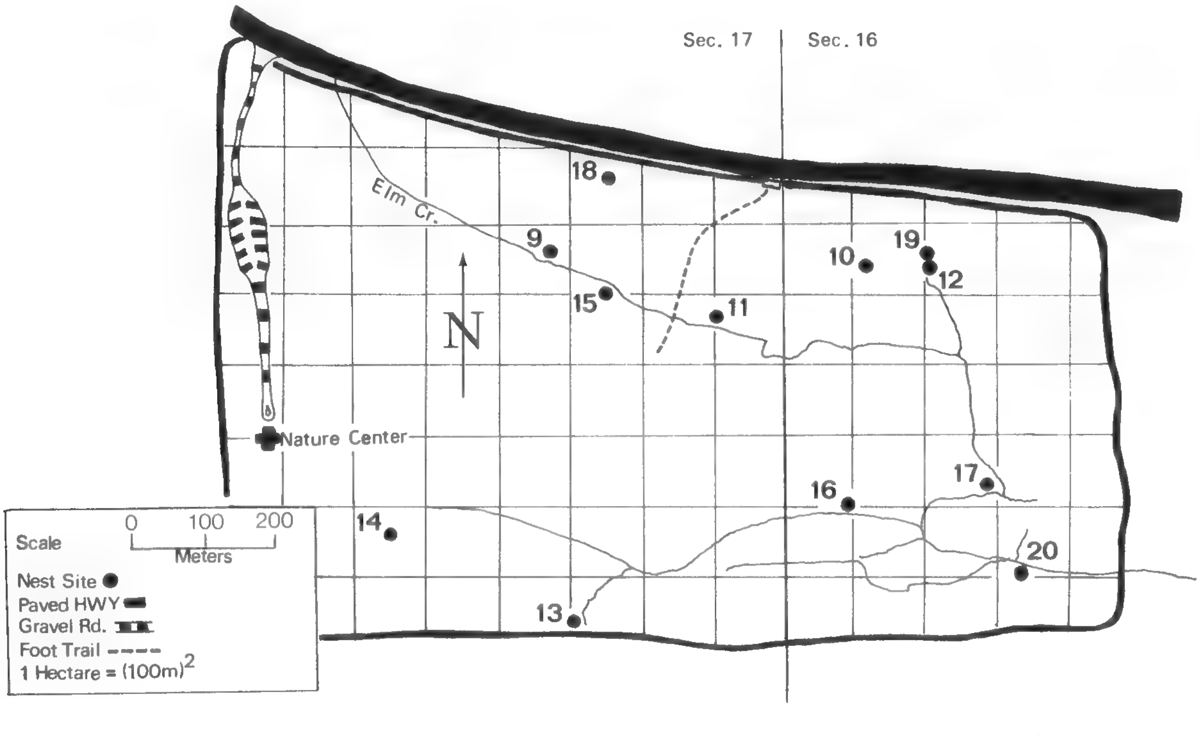

Figure 3. The study area in Neithercut Woodland, Clare County, Michigan in 1973.

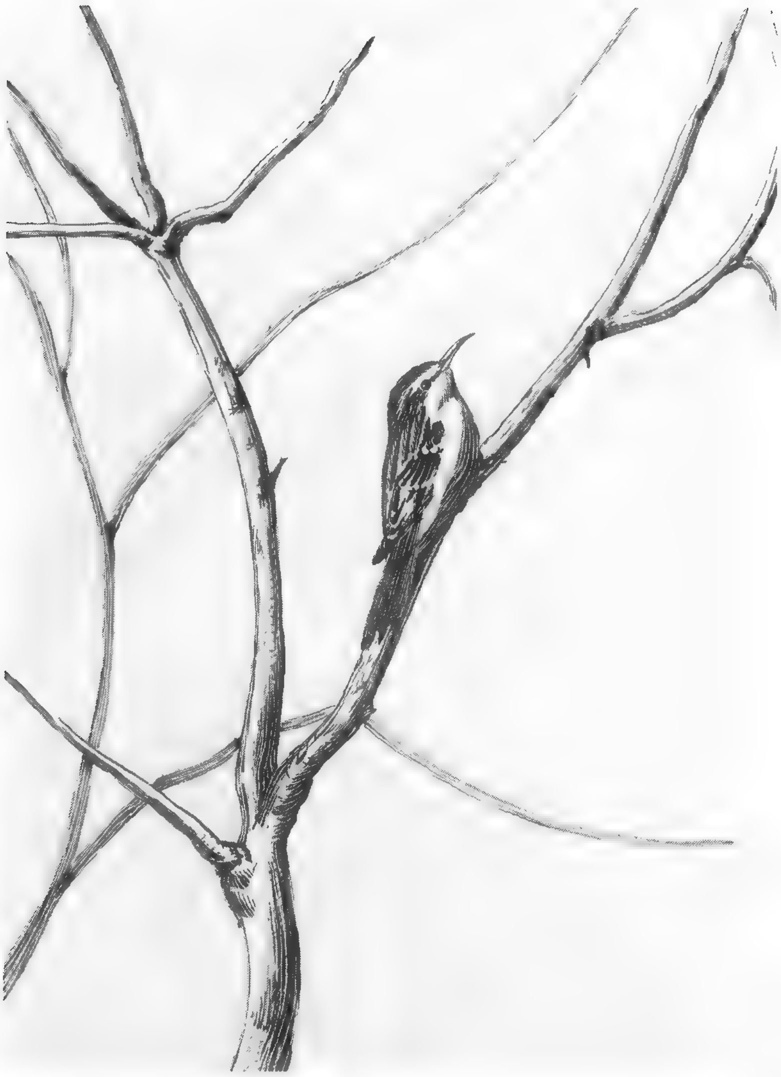

Figure 4. Males often sang from vertical perches near the tops of trees when establishing their territories. Drawing by Michael DiGiorgio.

tree trunks. Wing fluttering is often associated with courtship feeding. Lack (1940) states that Brown Creepers in Europe (?) regularly perform courtship feeding throughout the nesting cycle, presumably to maintain the pair bond. The female assumes a position similar to that of begging young on a tree trunk. She gapes and the male then places food in her throat.

All courtship activities that I observed occurred during periods when pairs quietly foraged from one tree trunk to another. In foraging, the birds started near the bottom of a tree, moved up and around the trunk with a jerky series of hops, legs spread wide to the sides of their bodies, tails pressed to the bark beneath for support after each hop, until, stopping, they turned slightly sideways and dropped to a lower level on the trunk or flew to the base of another tree. Call notes that kept the foraging pair together consisted of "*ts-ts-ts* ...," each note distinctly separated from the next by a short pause. Less frequent and softer was the longer, higher courtship note similar to that of a feeding Black-capped Chickadee *(Parus atricapillus)* and closely resembling the call of young, begging Brown Creepers.

I heard this courtship call before the quick, silent chases in which the two birds swerved among the trees approximately one to three meters apart, and landed on a tree trunk one above the other. With or without more begging notes, Wing-fluttering sometimes followed the chase (Figure 7). Wing-fluttering—a behavior involving rapid movement of wings held above the body—occurred with one or both birds fluttering in place or moving daintily up the bark, barely touching the tree with their feet. This courtship display lasted several seconds, often followed by another chase. Sometimes, after fluttering its wings, one bird fed the other. Generally, the male fed the female by landing above her and turning sideways to place the food in the throat of his mate (Figure 7). No copulation was observed during these courtship displays.

Through the ensuing nesting cycle, adult Brown Creepers continued their courtship displays and feedings. Courtship feeding terminated with the hatching of eggs when males began feeding begging young rather than unreceptive mates. Wing-fluttering continued after egg hatching, however, with food, and in the vicinity of their nest before feeding young. After fledging, young creepers attracted the adult birds with begging cries and fluttering wings, similar to the courtship notes and Wing-fluttering of courting adults. Older fledglings chased their parents to obtain food from them. Like courtship chases, the birds flew from tree to tree, until the older bird stopped, turned sideways, and fed the bird below.

The Nest

Searching for Nest Cavities

I briefly observed cavity searching activities at Neithercut six times from 7 April to 2 June 1973, in which pairs of creepers examined cavities created by bark separating from dead trees. I saw what I believed to be the same pair of birds searching for a nesting cavity three times. On 14 April I viewed the male for 12 minutes as he perched on a piece of elm bark still clinging to the tree. After looking behind the bark several times, he moved around in back of the bark, flew out 15 seconds later, and sang one song as the female flew to the same piece of bark. She momentarily tapped on the bark with her bill, then sidled to the edge and around between the bark and the tree trunk. She quickly reappeared on the outer bark and flew in the direction of her mate.

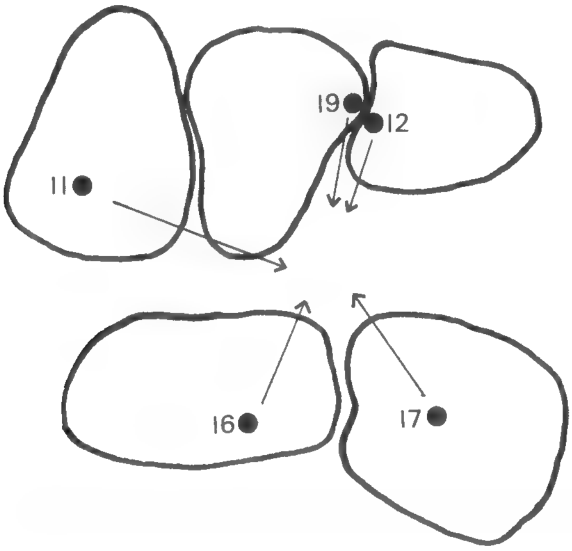

Figure 5. Location of intraspecific competition where established territories loosely adjoined, 5 June 1973 at Neithercut.

The birds jointly explored three additional cavities beneath American elm bark before they flew out of sight. I watched the birds checking other cavities for seven minutes on 23 April. Both birds examined different pieces of loose elm bark at the same time. I watched a pair, presumably the same birds seen earlier, searching for cavities while working at nest construction on 2 June. The nest was completed by 4 June.

The Nest Site

The Brown Creeper is known to nest beneath bark scales of many different tree species including those below compiled from the literature.

Species	*Literature citation*
American chestnut *(Castanea dentata)*	(Chadbourne, 1905)
American elm *(Ulmus americana)*	(Davis, 1976)
Baldcypress *(Taxodium distichum)*	(Widmann, 1895)
Balsam fir *(Abies balsamea)*	(Brewster, 1879)
Black and white oak (*Quercus* spp.)	(Tyler, 1914)
Northern white cedar *(Thuja occidentalis)*	(Chadbourne, 1905)
Incense cedar *(Libocedrus decurrens)*	(Bent, 1964)
Jack pine *(Pinus banksiana)*	(Parmelee, 1975)
Large-toothed aspen *(Populus grandidentata)*	(Davis, 1976)
Monterey pine *(Pinus radiata)*	(Legg, 1966)
Red maple *(Acer rubrum)*	(Parmelee, 1975)
Silver maple *(Acer saccharinum)*	(Hall, 1963)
White pine *(Pinus strobus)*	(Braaten, 1975)

At Reese's Bog dead balsam fir served as nesting sites for all but one pair of creepers. This exception was on a large-toothed aspen at the edge of a small swamp surrounded by other living large-tooth aspen.

At Neithercut there were numerous large-toothed aspen, dead and

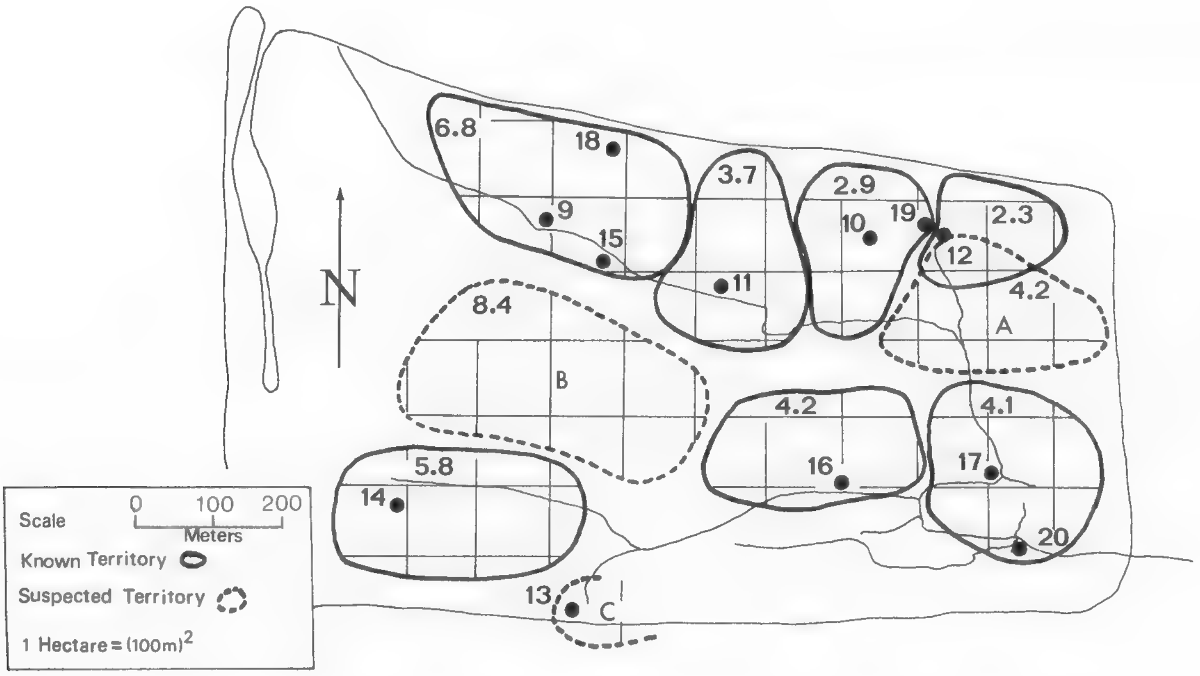

Figure 6. Brown Creeper territories at Neithercut Woodland. Multiple nesting in any one of these territories was the result of renesting attempts following nesting failures.

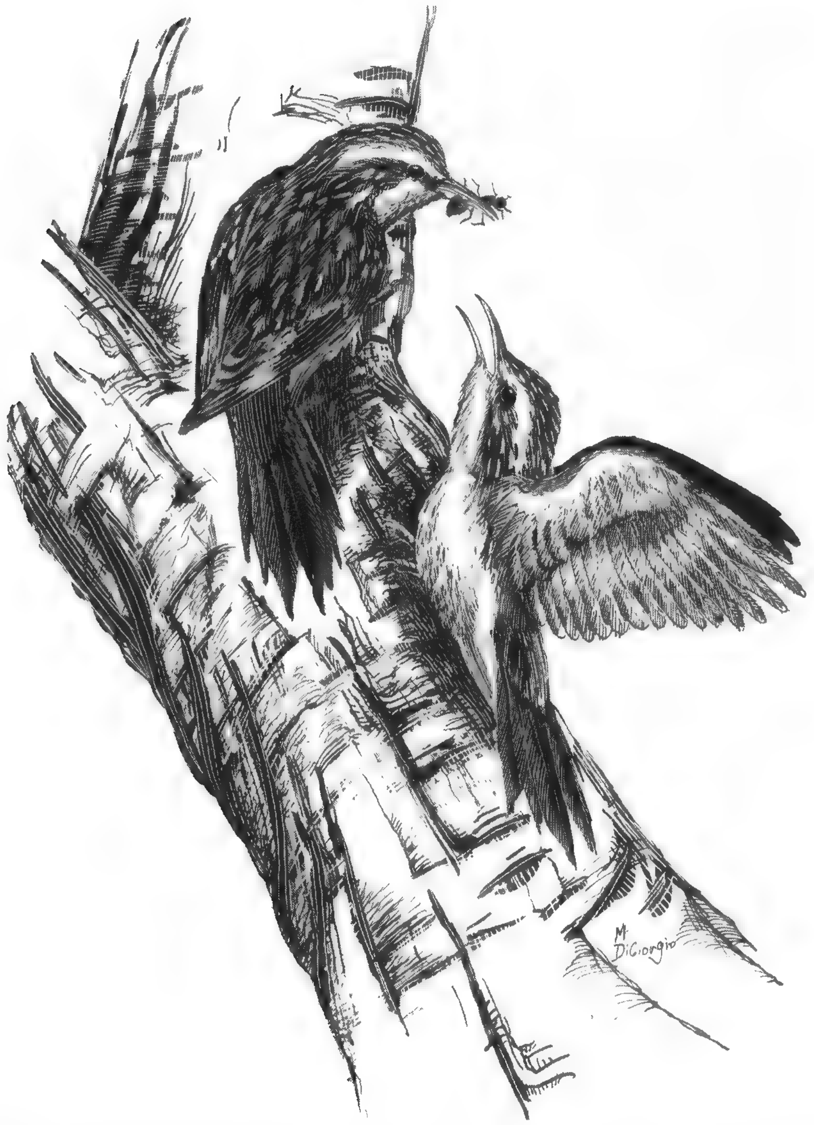

Figure 7. Wing-fluttering is one of the displays of courtship. Here the female Wing-flutters while being fed by the male after a chase. Drawing by Michael DiGiorgio.

dying from crowding by the more shade-tolerant red maple and American beech. The Brown Creepers, however, built their nests on the more abundant trunks of dead American elm. The elm bark was stronger and closer grained on its inner surface than the aspen bark, which tended to shred with age.

Each nest was on a dead tree, wedged under a piece of bark still loosely attached to the tree. Inner tree bark, to the front of the nest, was rough, light-colored, and free from dirt and rotting material. Wood to the back of the nest was smooth but also light-colored and free from dirt and rotting material.

Each nest tree was near water. Two of the nest trees at Neithercut stood in swamps; all other nest sites were not more than 60 meters from flowing streams.

Openings in the surrounding tree canopy permitted light penetration to each nest site, either because of surrounding dead trees (Neithercut) or from a road opening, swamp clearing, or the position of the nest tree on a stream bank (Reese's Bog).

Tree diameters, nest heights (measured to the upper edge of nest cups), and the length of bark scales under which the birds built their nests ranged widely (Table 1).

TABLE 1

Nest Tree Measurements

Nest number	*Tree species*	*Study area*	*Diameter at dbh (cm)*	*Nest height (m)*	*Bark scale length (cm)*
2	Large-toothed aspen	R.B.*	28	1.7	90
1	Balsam fir	R.B.	31	1.6	111
3	Balsam fir	R.B.	25	1.5	56
4	Balsam fir	R.B.	18	3.5	180
5	Balsam fir	R.B.	18	3.2	22
6	Balsam fir	R.B.	21	1.8	72
7	Balsam fir	R.B.	24	2.0	43
8	Balsam fir	R.B.	15	4.6	70
9	American elm	N.W.†	22	3.3	28
10	American elm	N.W.	33	7.0	257
11	American elm	N.W.	23	6.0	116
12	American elm	N.W.	56	3.0	33
13	American elm	N.W.	20	1.8	291
14	American elm	N.W.	20	2.9	40
15	American elm	N.W.	18	3.7	35
16	American elm	N.W.	18	2.6	28
17	American elm	N.W.	19	2.1	83
18	American elm	N.W.	31	1.6	104
19	American elm	N.W.	26	2.9	30
20	American elm	N.W.	26	4.9	55
Means	Balsam fir		22	2.6	79
Extremes	Balsam fir		15–	1.6–	22–
Means	American elm		26	3.8	100
Extremes	American elm		18–	1.6–	28–

*Reese's Bog
†Neithercut Woodland

Nest Building

Beneath a loose piece of bark, the creeper's nest adheres to the rough inner surface by means of the binding of twigs, pieces of bark, and the bark scale with spider egg cases and insect cocoons. Although it fills the space between the bark and tree trunk, the nest does not adhere to the smoother trunk. Twigs and strips of bark form the base of the nest, which is a hammock-shaped collection of layered materials with "horns" that extend up above a central nest cup. The nest cup (which can often be removed from the total nest without disturbing its construction or that of the base materials) lies on top, and to the center, of the base and is made of finer bark and wood fibers.

Both male and female creepers may carry nesting materials, yet the nest is primarily built by the female.

I found that base materials are gathered one at a time, pulled from various trees and shrubs in a radius of approximately 100 meters from the nest. Finer nest cup materials are gathered in tufts. When finished, the upper edge of the nest receptacle may lie 15 centimeters (N11) below the cavity entrance level.

Nests were built beneath bark where cracks and holes permitted the birds to enter small spaces between the bark and tree trunks.

The base materials used in nest construction reflected the location (Table 2). At Reese's Bog nest bases beneath balsam fir bark consisted of balsam fir twigs and strips of white cedar bark. The one nest built under a piece of large-toothed aspen bark was formed from fibrous strips of the inner aspen bark. Nest bases beneath American elm bark consisted of pieces of bark from American elm, eastern white cedar, and paper birch, and twigs from red maple and eastern hemlock. At both study areas insect cocoons and spider egg cases were twisted about and adhered to these base materials and to the inner bark scales.

The size of each nest base conformed to the size of the nesting crevice. The most extensive base was 355 mm deep, 165 mm wide, and 63 mm thick. Taken apart after the nesting season, this nest (N18) base consisted of 872 pieces of material.

During periods of observed nest building by one pair, only the female gathered materials for the base. She pulled at pieces of bark and twigs with her bill and gleaned cracks and crevices for spider egg cases and insect cocoons. Once she fluttered in midair to pry a piece of bark loose from a tree. She carried one piece of material at a time to the nest from trees in the vicinity of the nest. After remaining at the nest for up to 30 seconds, she flew out to obtain more material. During early nest base construction, several pieces of nesting material fell through the nest bottom. The female creeper made no attempt to retrieve them from the ground. During a two-hour observation period she carried 40 pieces of elm bark into the nest.

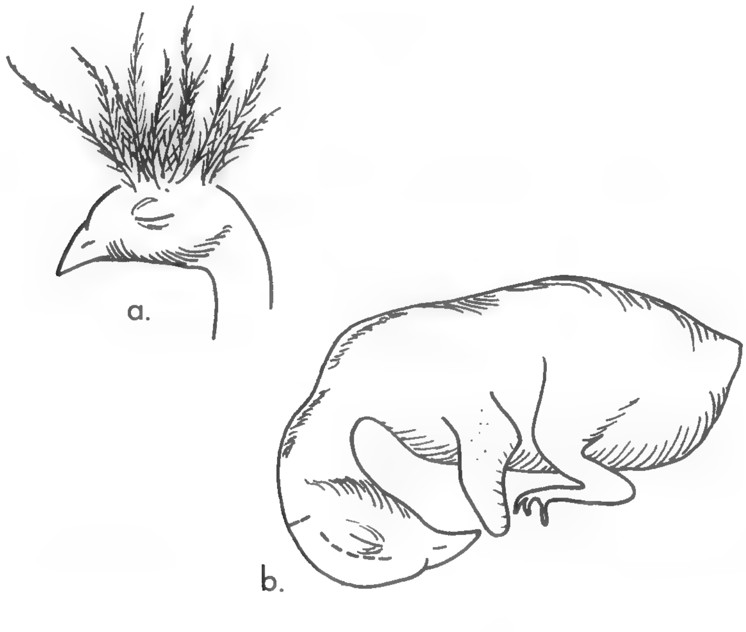

Figure 8. First-day nestling showing (a) natal down, and (b) superciliary and occipital positions of the natal down after the nestling's head was plucked.

Nest cups consisted of fine, usually light-colored bark and fine wood fibers. I saw females of four nests (N5, N10, N11, and N18) bringing these finer materials to their nests in tufts that extended out the sides of their bills. One female (Nest N11) gleaned a dead eastern hemlock branch at the base of the nest tree. Another female (Nest N18) collected fragments from an eastern white cedar and small, gray strips of eastern hemlock and paper birch bark. The nest cup (N18) also contained 15 spider egg cases.

While the female birds collected the materials, their mates sang close by. One male (Nest N18) often followed the female back and forth to the nest tree. In the immediate vicinity of the nest he occasionally fed the female. He

TABLE 2

Amount of Materials Found in the N18 Nest Base

Material	*Size*	*Amount*
Fine twigs (eastern hemlock)	30–100 mm long	246
Course bark (American elm, eastern white cedar, red maple, and eastern hemlock)	10–90 mm long 10–20 mm wide	214
Fine bark (white birch)	10–60 mm long 2–10 mm wide	206
Silk (of insect cocoons and and spider egg cases)	Long, unmeasured strands and small masses	124
Coarse twigs (white birch and red maple)	14–140 mm long	74
Hair	160–230 mm long	3
Wood chips	30–50 mm long 10–20 mm wide	3
Grass	50 mm long	1
Leaves	Fragmented	1
Total		872

TABLE 3

Nest Dimensions (mm)

Nest number	*Nest base*		*Nest cup*	
	Width	*Thickness*	*Depth*	*Width*
N5	200	85	37	110
N12	180	105	63	130
N13	158	44	34	145
N17	127	60	44	157
N18	165	63	28	138
Means	166	71	41	128
Extremes	127–200	44–105	28–63	110–145

often entered the nesting cavity behind her, coming out less than a minute later, just before the female left the nest.

Measurements of five nests, where nearly accurate dimensions could be obtained (Table 3), showed that nest cups closely conformed to the size of the bird. The distance across the nest cup depression, parallel to the bark, ranged from 31 to 57 mm. The nest cup depression depth ranged from 28 to 63 mm.

Length of Nest-building Periods

Harrison (1975) states that nest building may take a month of intermittent construction activity. Nest-building periods in this study were about six and seven days long for two nests (N19 and N18, respectively). One of these nests (N19) was a second attempt by the pair of birds that had built and abandoned a nest (N10) sometime after 12:35 on 31 May. I recorded one egg in Nest N19 by 07:00 on 6 June. The pair that built Nest N17 began building sometime after their previous, and second, nest (N15) was destroyed during the night of 27 May. One egg rested in Nest N18 by 07:30 on 4 June.

Since Nests N19 and N18 were second and third nesting attempts and were small- to medium-sized nests, respectively, other nests probably took longer to build. Pettingill (1970) stated that, judging from the few known records of the length of nest-building activities, second or third nests in the same season built by the same pair of birds take less time than do their first nesting attempts.

Egg Laying

Egg laying began the morning after completion of the nest. Each female apparently laid one egg a day in early morning hours. There was one egg in N5 at 18:45 on 20 June 1971 and no adult was present. Two eggs were in the nest on 21 June at 05:30. The female re-entered the nest and stayed from 05:59 to 06:05, but no additional egg was laid. There were three eggs by 10:10 on 22 June; four eggs on 23 June; and the fifth and final egg was in the nest on 24 June.

Clutches of 11 nests varied from 4 to 7 eggs (Table 4). The most common clutch size was six eggs (six nests). This norm was the same as recorded in Bent (1964), although he reported clutches of up to eight eggs. I recorded two cases of double clutches in the same season by the same female. In both, the first clutch was larger than the second. Thus, the first set of eggs (N10) by one female was six eggs; her second clutch (N19) was five. In another instance, a female that laid six eggs (N15) earlier in the season, later followed up with a second set (N18) of four eggs.

Eggs are white, covered with rufous-red spots and blotches circling the larger, blunt end. Two eggs from an abandoned nest (N13) measured 15 by 12 mm; one weighed one gram, the other 0.8 gram.

Incubation

Females did all of the incubating during a total of 15 hours of recorded observations at eight nests. Harrison (1975) and Bannerman (1953) state that both sexes incubate.

Incubation apparently began after the clutches were complete.

Females incubating six eggs arranged them in two rows of three, lengthwise.

Attentive intervals varied widely, lasting up to 82 minutes. Comfort movements could be seen at times as the tail swung up, down, and from side to side. Females occasionally reversed positions while in their nests.

Males brought food to their incubating mates, rendering song and/or courtship call notes as they approached the nest. Females left the nest after males gave the high courtship note several times in the immediate vicinity. Females answered the call notes and sometimes flew to the male, Wing-fluttered briefly, and accepted a food item from the male. At other times the male flew to the female, sidled down a tree trunk to her, fed her, fluttered briefly, and then flew to another tree. The females either returned immediately to their nests or foraged with their mates for up to 27 minutes.

Using clutches (N18 and N19) I had color-marked sequentially, I measured the length of incubation periods from the laying of the last egg until the hatching of that egg. Both nests had 15-day incubation periods (Table 4). The last egg laid in N19 hatched before the first egg. Incubation periods of clutches that were not color-marked for identification ranged from approximately 15 to 17 days. Bannerman (1953) lists the Brown Creeper's incubation period as 14 to 15 days.

Development of the Nestling

Immediately after hatching, young creepers were blind, pink-bodied, and practically naked except for dark gray natal down on their heads (Figure 8a), arranged in three rows of six feathers each. There was one row above each eye and one row running across the occipital region of the head (Figure 8b). These feathers measured 9 to 10 mm in length. The day-old young (Nest N12) measured from 30 to 34 mm in length when extended. The outline of development was as follows: On the second day after hatching the outline of the spinal feather tracts showed as thin lines of tiny gray dots. By Day 5 the spinal feather tracts were black and approximately 1.5 mm wide. The incipient feathers of the alar tracts made their appearance as black dots. On Day 6 the eyes were still closed and each side of the gape was white, thick, and fleshy in appearance. There were unopened, black pin feathers in both the auricular and loreal regions of the heads. The ventral feather tracts were dark and about 1.5 mm wide. Spinal tract pin feathers were ready to break through their sheaths and alar feathers had begun to emerge from their sheaths. These tiny tufts of juvenal feathers gave the young a slightly brownish appearance.

On Day 7 the wings appeared blackish-gray with a slight brown cast as the juvenal feathers continued unfolding. Skin color of the apteria was red instead of pink.

On Day 8 eyes were open and the sides of the gape were more yellow than white. Juvenal feathers on the spinal tracts were unfolded. Rectrices were just breaking from their sheaths. Unopened pin feathers projected from the coronal regions of the head.

On Day 9, food cries from the young in N19 could be heard faintly from three meters away as the parent birds landed on the nest bark. The night of Day 10 was the first that young in N11 were not brooded. The nestlings huddled close together in the nest cup with feathers fluffed especially at the shoulders. By Day 11, brown and white feathers and white wing bars were

TABLE 4

Clutch Sizes and Incubation Periods

Nest number	*Clutch size*	*Start of incubation*	*Hatching date*	*Duration of incubation (days)*
1	4	—	16 June 1971	—
5	6	30 June 1971	14 July 1971	15
7	5	—	5 July 1972	—
10	6	—	—	—
11	6	20 May 1973	6 June 1973	17
12	6	—	5 June 1973	—
14	6	20 May 1973	3 June 1973	15
15	6	22 May 1973	—	—
17	7	7 June 1973	—	—
18	4	7 June 1973	21 June 1973	15*
19	5	10 June 1973	24 June 1973	15*

*Incubation periods determined with marked eggs.

visible. There were unopened sheaths still under the birds' chins. The young were restless, bills still pointed up, and bodies just reached the top of the nest cups.

By Day 12, nestlings began climbing briefly above the nest cups. They climbed and sidled down the inside bark and tree trunks forming the nesting cavities. The young held their tails (now about 12 mm long) spread outward and pressed down on the bark while maintaining their positions. From over eight meters away I began regularly hearing begging *chees* notes when the adult birds touched the bark. Nestlings began poking their heads out of the nesting cavities for food.

On Day 13, climbing continued during daylight hours and was still limited to the internal cavity. Young were more restless than on previous days. At night nestlings returned to the nest cup and huddled together with feathers fluffed.

On Days 14, 15, and 16, activity at the nest was intense. The young frequently preened their breast feathers. They scrambled up, down, and over one another. They frequently fluttered their wings beneath the bark and at the cavity entrances when they reached out for food. The nestlings were fluffy, mottled-brown, with a little natal down still clinging to juvenile feathers on their heads. There still were yellow swellings at the sides of the gape. Though fully-feathered, these nestlings huddled together for warmth on cold days and at night in tight groups on the inner bark scales.

Parental Care

Brooding

Only females brooded young. The duration of brooding bouts depended on the weather and the age of the nestlings. Brooding periods lasted as long as 35 minutes per hour in a nest (N7) of five young at two days of age. In a nest (N2) of four young at 12 days of age, I recorded only four brooding periods, each 1 to 2 minutes, during an all-day observation.

Feeding Young

Both adults fed young soon after hatching. Ants were included in the diet. Six-day-old nestlings received the first discernible moths. By ten days of age the young creepers' diets included click beetles, harvestmen, and mayflies. When the nestlings (N19) were 12 days old, I watched the adult male pluck a spider off its web and carry it to the nest.

The adult Brown Creepers gathered this food at the nest site and at distances up to 150 meters or more from the nest tree. They mainly gleaned tree bark, searching furrows, ridges, and cavities for insects and arachnids. They fed one nestling per feeding trip.

TABLE 5

Number of Feeding Trips to Nest (N2)
with Four Twelve-day-old Nestlings (15 June 1971)

Time of day	*Number of feeding trips*			*Total*	*Comments*
	Male	*Female*	*Unidentified*		
04:00–04:59	1	2	—	3	Feedings started at 4:52; male sang 2 songs
05:00–05:59	7	7	—	14	Male sang 2 songs
06:00–07:00	8	13	1	22	Male sang 4 songs; female brooded 20 sec.
07:00–08:00	5	10	11	26	
08:00–09:00	6	10	—	16	
09:00–10:00	9	7	1	17	Male sang 1 song
10:00–11:00	10	7	6	23	
11:00–12:00	3	7	2	12	Adults away from nest 22 min.
12:00–13:00	9	11	—	20	
13:00–13:59	7	11	—	18	Female brooded twice, one period 60 sec. long, the other 158 sec. long
13:00–14:00	4	5	4	13	Adults away from nest 29 min.
14:00–15:00	8	4	2	14	
15:00–16:00	5	9	3	17	
16:00–17:00	9	12	2	23	
17:00–18:00	6	10	1	17	Female brooded twice, one period 144 sec. long, the other 68 sec. long
18:00–19:00	9	10	—	19	Male sang 2 songs
19:00–20:00	—	1	—	1	Last feeding at 20:12
Totals	106	136	33	275	Male sang a total of 11 songs Female brooded 7.5 min.

In the food gathering process, the adult birds stabbed, shook, and rearranged active insects.

During an all-day observation of Nest N2 on 15 June 1971, when the nestlings were 12 days old, the adult birds made 275 feeding trips to the nest from 04:52 to 20:12 (Table 5). The female made 136 (49.5%) of these trips, the male 106 (38.5%), and on 33 (12%) trips to the nest, I could not determine the sex.

Intervals between feeding trips varied from 1 to 29 minutes, as first one adult, then the other, fed nestlings one to six times before the other adult carried food to the nest. There was one break of 22 minutes (10:55 to 11:17) and one of 39 minutes (14:38 to 15:07) when both adults left the vicinity of the nest.

Feeding trips decreased somewhat during midday observations. Thus, the number of feeding trips averaged 21 per hour from 6:00 to 11:00 hours, 16 per hour from 11:00 to 17:00, and 20 per hour from 17:00 to 20:00.

Disposal of Fecal Sacs

As Brown Creepers throughout the study areas left their nests to search for food, they frequently picked up a fecal sac from the nest or more commonly caught the sac as a nestling raised its tail and emitted the sac from its cloaca. The adult carried it in its mandibles to a tree where, with one quick movement of the bill, the fecal sac was slapped on the bark where it stuck.

I recorded a Brown Creeper eating fecal sacs only at one nest (N1); the nestlings were one day old. At this nest, the female ate a fecal sac just before leaving the nest. Fourteen minutes later the male carried a fecal sac from the nest and fed it to the female as she begged on a nearby tree trunk.

Fledging and Post-fledging Behavior

Fledging occurred 15 to 16 days after hatching (Table 6), varying slightly from Bannerman's (1953) estimate of 14 to 15 days in Great Britain and Bent's (1964) 13- to 14-day average in North America. I directly observed the fledging process at only one nest. At ten additional nest sites I saw fledged young within 24 hours or less after recording them in the nest.

Six young fledged from Nest N16 over a period of 57 minutes (14:20 to 15:17) at 1- to 28-minute intervals on 6 June 1973. The first nestling must have fledged before my observations began at 13:00, since seven nestlings were in the nest through 5 June and roosted together as fledglings on 7 June. The second young fledged at 14:20, the third at 14:33, the fourth at 14:35, the fifth at 15:03, the sixth at 15:16, and the seventh at 15:17.

During the fledging period, adult Brown Creepers fed young that were still in the nest and removed their fecal sacs from the nest; they also fed those young which had fledged.

There was almost constant communication between adults, nestlings, and fledglings in the form of location call notes and begging cries. All sound stopped once when the adult birds momentarily followed a low-flying Blue Jay *(Cyanocitta cristata).*

The young left the nest by means of various openings. All fledglings flew shakily down from the nest tree and alighted on other tree trunks from three to six meters away. In the air their wings made a series of short *whit* sounds. As soon as they alighted they began climbing upward with a series of short,

TABLE 6

Ages at Fledging

Nest	*Number of nestlings*	*Hatching date*	*Fledging date*	*Age at first flight (in days)*
1	4	16 June 1971	2 July 1971	15
4	6	14 July 1971	30 July 1971	16
7	5	5 July 1972	21 July 1972	16
14	6	3 June 1973	18 June 1973	15
18	3	21 June 1973	7 July 1973	16
19	5	24 June 1973	9 July 1973	15

jerky hops. Between hops they used their short tails for support against the bark.

For 25 minutes after fledging, the young grouped and regrouped on the dead elm trunks within a twenty-meter radius of the vacated nest.

During the next 49 minutes, the seven young creepers formed two groups on separate, but nearby, dead elms. There they preened and begged to be fed, their red mouth linings conspicuous. The parents responded during this period with 50 feedings.

For the next 83 minutes (16:37 to 18:00) I recorded 65 feedings and heard continual begging cries from the young, call notes from both adults, and five songs from the adult male.

Both adults fed the group a total of 19 times from 20:42 to 21:21. The female brought in more food items than did the male, which sang seven songs and flew to the group at least five times without food.

This was the only time I recorded the removal of fecal sacs from the roosting fledglings. The adults took four sacs consecutively from the young and flew off with them to nearby tree trunks where they wiped the sacs off on the bark.

The adults left the area for the night at 21:21. The sun set at 21:35 and the young were silently huddled together when I departed at 21:40.

The next morning (7 June) both adults fed the young where they had grouped together the night before. From 06:28 to 07:20 the seven young remained loosely grouped and received 41 feedings. This roost was abandoned by 07:25, when young flew to nearby trees and were fed.

It was often possible to locate family groups from the various nests (N11, N14, N16, N18, and N19) by sound. A continuous exchange of begging, *chee* notes, short flight *chips*, and longer location call notes most often marked the birds' positions. Infrequently, a male's singing led to the discovery of a family group.

Such groups were always seen within approximately a 500-meter radius of their former nests. The birds usually frequented the same territorial areas where adult males sang while females incubated eggs and where, later, both adults collected food for their nestlings. Three family groups (N11, N16, and N19) foraged in territorial areas formerly maintained by adjacent nesting pairs (Figure 9).

Fledglings actively begged for food for periods ranging from 5 to 64 minutes. They fluttered their wings with mouths gaped as they turned toward an approaching adult. Frequently the birds separated in two distinct feeding groups, one fledgling group following one parent, a second group following the other.

Between active feeding periods young fledglings rested singly or in groups for intervals of 2 to 95 minutes. They rested from three to ten meters above the ground, pressing their bodies against the bark and tails down and spread against the bark for support. With equal frequency, they rested just below a tree crotch, under a limb, or on a straight vertical tree trunk. The birds kept to the side of the trunk opposite strong, chilling winds.

When an adult alighted on the roosting tree above the young, one or two young would push to the top of the group or flutter up the tree, receive food, then drop down to the resting group. When an adult landed below the fledglings, one or two begging young frequently sidled to the bottom of the group.

The N14 young were fed 31 times while resting from 16:00 to 17:00 hours on the day they fledged (18 June 1973). They were fed 35 times when actively begging from 17:00 to 18:00 hours the next day.

Adult creepers never joined the resting groups.

Roosting

Night roosts formed as birds in resting groups drew closer together (Figure 10). Perimeter birds turned inward, forming a tight, flattened, circular patch of birds. Heads were not visible and the birds appeared very fluffed about their necks and shoulders. Only once did I see a bird with its head turned and its bill inserted under its scapular feathers.

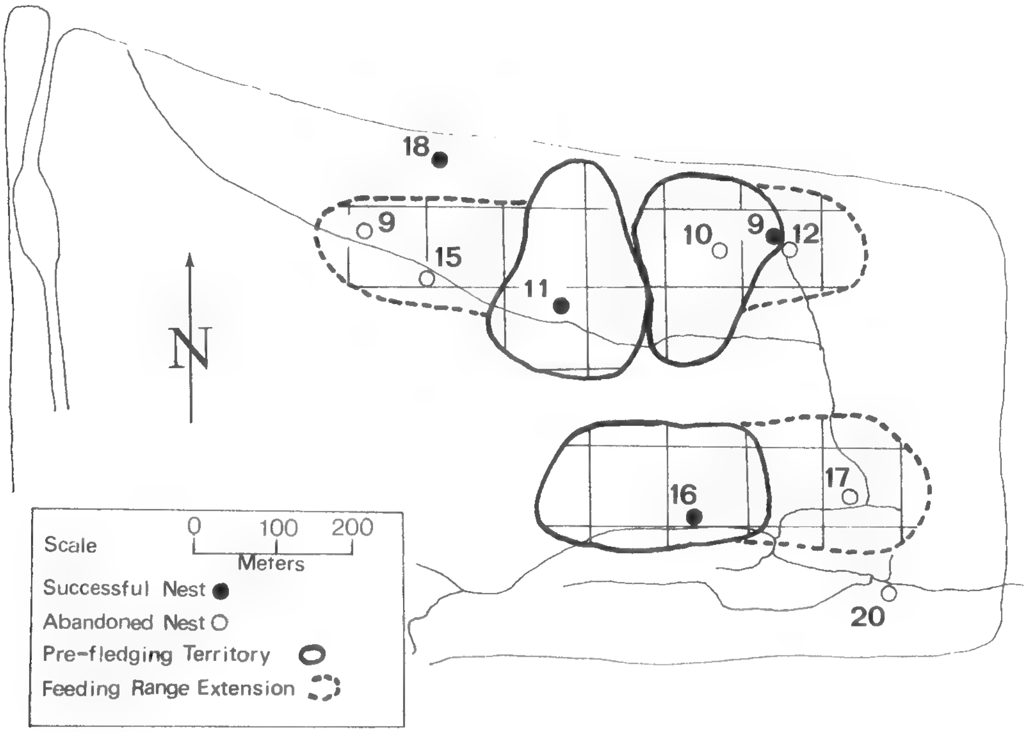

Figure 9. Feeding range extensions after the young in Neithercut Woodland fledged and moved into territories formerly maintained by other nesting pairs of Brown Creepers.

The roosting birds resembled descriptions by Lohrl (1955) of winter sleeping aggregations of Short-toed Treecreepers *(Certhia brachydactyla)* in Germany. However, the winter sleeping roosts in Germany each consisted of up to 20 birds (evidently more than one family group) and the same roosting sites were used repeatedly. Night roosts seen at Neithercut consisted of only the young birds of a single family group and the same site was never used more than once. The birds roosted where they were at about 21:00 each night, selecting spots in the shadows of other trees where it was difficult to make out the outline of the birds in the evening or morning light.

A gradual restlessness developed at the roost in the early morning hours. The birds separated somewhat and perimeter birds turned outward. Adult feedings initiated short, individual flights by fledglings that terminated back in the group. Begging cries increased, as did preening and stretching.

Young creepers left the roost suddenly as first one, then others, quickly flew to different trees in the general vicinity of the first young to leave the group.

Anti-predator Reactions

Adult Brown Creepers were silent and motionless when potentially dangerous situations developed in the nesting areas. A pair of Sharp-shinned Hawks *(Accipiter striatus)* built their nest in a white pine 300 meters from a nest (N1). When one of the hawk's screams was heard at the nest, the adult creepers ceased calling to each other and the nestlings stopped beg-

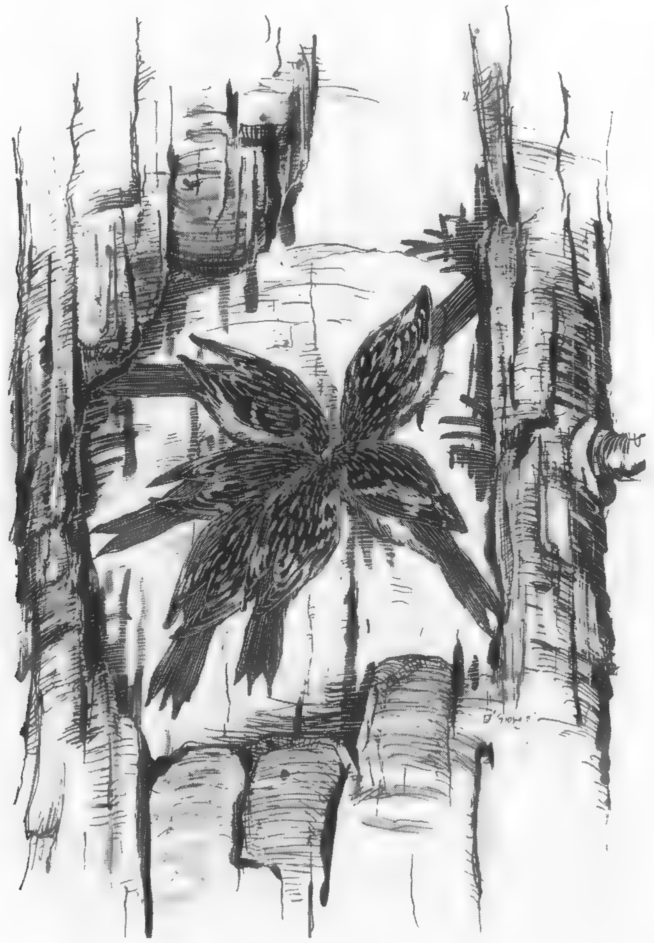

Figure 10. Night roosting position of fledged Brown Creepers, resembling winter sleeping aggregations of Short-toed Treecreepers in Germany. Drawing by Michael DiGiorgio.

ging. The parents "froze" with their bodies pressed against tree bark for several minutes before resuming their activities.

The pair at another nest (N19), containing nestlings that were six days old, reacted similarly when a Green Heron *(Butorides virescens)* landed in the top of the nest tree. The female pressed her body against the bark scale covering the nest until the heron left.

Even newly fledged young pressed their bodies against the bark of a tree trunk as a reaction to the scream of a hawk. One young creeper, approximately two hours after fledging, suddenly stopped and flattened out against the bark of a white pine as a White-breasted Nuthatch *(Sitta carolinensis)* faced down the pine four meters above the creeper. The latter stayed there for 17 minutes until the nuthatch left.

Young creepers were lunged at by Scarlet Tanagers *(Piranga olivacea)*, American Robins *(Turdus migratorius)*, and even White-throated Sparrows *(Zonotrichia albicollis)* when they unwarily ventured into the nesting territories of these species.

Development of Fledglings

First-day fledglings moved relatively little, only up to eight meters per hour.

Second-day fledglings were more scattered and moved faster and farther per flight. They began to nibble hesitantly at objects on bark surfaces.

Third-day fledglings actively followed adults for longer intervals between resting periods.

Nine-day-old fledglings gleaned the bark themselves, but the major portion of their food still came from the parents. The young followed adults up tree trunks and begged continually until fed. A young creeper often stayed in one place after being fed as the adult carried two or three additional food items to it.

These older fledglings often moved out of sight behind a tree trunk when approached. They "played" in the air by spiraling around the base of a tree. Each time a bird alighted it flicked its wings and took off again in seconds. Sometimes two fledglings chased each other.

Eleven-day-old fledglings quietly foraged for themselves more than they begged from adult birds.

At seventeen days, young creepers still begged at times and were fed. They persistently followed adults to various trees until the older birds relinquished food items.

From mid-July through October I did not find family groups and saw no more than two Brown Creepers on most occasions. Bent (1964), however, reports that young of the year are attended by adults up to the first week in September.

Nest Success

Eleven (58%) of the 19 nests containing at least one egg or nestling succeeded in fledging young (Table 7). Of a total of 94 eggs laid, 56 hatched, and 49 young fledged.

Two successful nests (N2 and N3) fledged young on the same day within 100 meters of each other. At Neithercut Woodland the closest successful nests were 221 meters apart; but in one nest (N11) the young fledged three

TABLE 7

Nests Containing at Least One Egg or Young

Nest number	*Number of*			*Loss due to*
	Eggs	*Nestlings*	*Fledglings*	
1	4	4	4	
2	4	4	4	
3	4	4	4	
4	6	6	6	
5	5			Desertion
6	5			Predation
7	5	5	4	
8	?	?	?	
10	6			Desertion
11	6	6	6	
12	6	6		Predation
13	3			Desertion
14	6	6	6	
15	6			Desertion
16	7	7	7	
17	7			Predation
18	4	3	3	
19	5	5	5	
20	5			Desertion
Totals	94	56	49	

weeks ahead of the other (N18). There were no renesting attempts after a successful nesting.

At Neithercut Woodland, 10 of the 11 nests containing at least one egg or young were found in either the nest-building or egg-laying stage of the nesting cycle. Twenty-seven of the 61 known eggs laid then resulted in fledglings. This represents a 44.8 percent fledging success. This success rate more closely approaches Nice's (1957) 45.9 percent egg-to-fledgling success for altricial open-nesters (based on a summary of 35 studies of the success of open-nesters), than it does her 66 percent success for altricial hole-nesting species (based on a summary of 20 New World and 13 Old World studies of the success of hole-nesters).

Causes of Nest Loss

Nest loss occurred three times as a result of alteration of the bark scale due to rain, once due to brood parasitism, three times due to predation, and twice due to human disturbance. Wind resulted in one additional nest loss.

Rain and Wind

Sixty percent of the nesting failures at Neithercut resulted from the effects of rain and wind. Because of the adhesion of nesting materials to the inner bark surface, several nests succeeded in fledging young in spite of severe warping of bark during periods of high rainfall.

Rain indirectly destroyed two nests (N10 and N15) and probably a third (N13). A long rainy period occurred from 7 May to 6 June 1973 with particularly heavy rains from 26 to 31 May. The rains were warm and humidity remained very high between storms. These weather conditions weakened the soaked bark nest scales and they began to pull away from the trees, exposing the adherent nests.

During the same rainy period the cavity entrance of one nest (N11) opened from 16 to 44 mm, placing the nest 20 to 30 mm away from the nest tree. During a short drying period the opening returned to 16 mm and the nest rejoined the tree trunk. The bark did not pull away from the nest tree in later rain storms.

During a wind storm on 26 July 1971, the bark scale with a nest (N5) attached to it was blown to the ground. The five eggs contained in the nest cup did not break in the resulting fall of 3.2 meters. Although clearly visible the following morning, the adults did not go to the nest; instead they searched the former nest location for about 45 minutes. They were not seen again in the area.

Brood Parasitism

One nest (N13) containing two eggs of a Brown-headed Cowbird *(Molothrus ater)* was abandoned by 15 May (Figure 11). The nest access fissure was very wide. The nest parasitism may have occurred after the fissure opened; or it is equally probable that the cowbird enlarged the entrance when gaining access to the nest. The parasitism of one nest by cowbirds is the only definitely known incident of its occurrence. Friedmann (1963) lists one

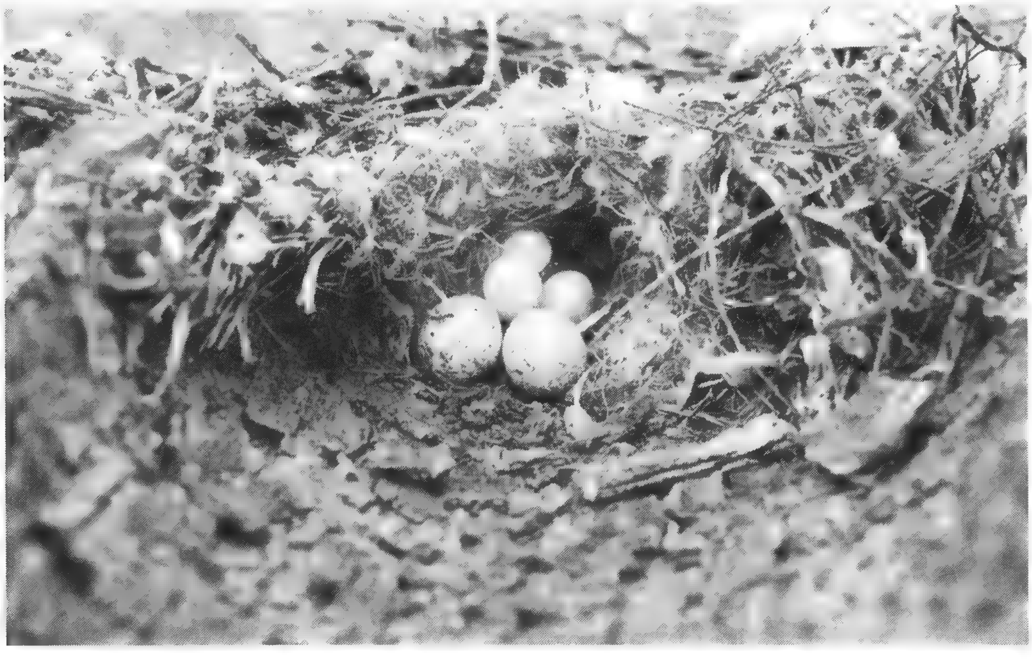

Figure 11. Nest site after protective covering of bark has been removed, showing the nest (N13) with two eggs of a Brown-headed Cowbird in addition to three creeper eggs.

probable instance of cowbird parasitism involving a pair of Brown Creepers seen feeding a fledged cowbird.

Predation

Several nests were destroyed by predators, but the animals could not be identified. Since Red Squirrels *(Tamiasciurus hudsonicus)* foraged daily in the area of one nest (N7), they may have preyed upon this nest. Materials forming the nest cup appeared dug from the nest; no egg shells remained in the vicinity of the nest tree.

The predator of Nest N17 was evidently small. It did not disturb the nesting material as it entered the nest and ate four of seven eggs. It left the shells in the nest. This predator did not return to the uneaten eggs nor did a Brown Creeper return to incubate the remaining eggs.

Nestlings, rather than eggs, served as food for the predator of Nest N12. I discovered three dead young in the nest. The other three day-old nestlings were missing. The nest cup showed little disturbance, yet one of the nestlings had a hole in its skull.

Human Disturbance

Two pairs abandoned their nests (N9 and N20) because of my disturbance at the sites. One female ceased building after being caught in a mist net. The other pair deserted their nest after I placed a ladder against the nest tree.

Population Changes

In this study, there was a marked increase in the number of Brown Creepers in Reese's Bog over the number found by Riggs (*in* Nelson 1956) 36 years previously. Riggs estimated two pairs of Brown Creepers per hundred acres (40 hectares) for the densely forested portion of Reese's Bog as compared with five pairs nesting in 17 acres (6.8 ha) in 1971. Undoubtedly there was not the same number of short-lived balsam fir at Reese's Bog at the same stage of decay in 1946 as in 1971, thus possibly accounting for the increase in Brown Creepers.

Likewise, at Neithercut Woodland there were many more creepers present than would be expected from Cuthbert's (1962) classification of this species as a rare summer resident of Isabella County (the northern boundary of which runs less than five miles to the south of Neithercut Woodland). There were at least eight pairs of Brown Creepers nesting in 195 acres (78 ha) at Neithercut in 1973. Neithercut Woodland is on the southern boundary of the Brown Creeper's known breeding range (A.O.U. Check-list of North American Birds, 1957) where, according to Pearson (1923), nests are placed nearly always behind bark of balsam fir. The nesting of the Neithercut creepers exclusively beneath American elm may allow a southern extension of the creepers' breeding range since woodlots in Isabella and more southern counties are similarly affected by the Dutch elm disease. If so, this may prove to be a temporary spread, since the elm bark falls completely off the trees.

Summary

I observed the Brown Creeper's nesting cycle as it related to feeding habits during nesting periods from June 1971 through July 1973 in Michigan's Lower Peninsula. Study areas included an area of Reese's Bog at the north end of Burt Lake and a section of Neithercut Woodland in Clare County. Reese's Bog is an old white cedar swamp. Neithercut Woodland is a more southern woodland presenting a wider variety of soil types and floral species.

Observations centered around 20 Brown Creeper nests found during various phases of the birds' nesting cycle.

Territorial singing occurred commonly at Neithercut in April, May, and early June, continuing until the young fledged. Males sang from vertical perches in the tops of trees while establishing territories. After territory establishment males more commonly stopped briefly to sing as they searched for food on lower tree trunks. Singing rates were directly proportional to the amount of observed intraspecific territorial competition in the nesting areas.

Territory size ranged from 2.3 to 6.4 hectares. Birds holding smaller territories engaged in more vocal defense than those with larger territories.

The Brown Creepers' courtship activities included display flights, courtship chases, Wing Fluttering, and courtship feeding. All courtship activities that I observed occurred during periods when pairs quietly foraged from one tree trunk to another.

Balsam fir and large-toothed aspen at Reese's Bog and American elm at Neithercut served as nesting sites. Each nest was on a dead tree, wedged under a piece of bark still loosely attached to the tree.

Nests were built beneath bark where cracks and holes permitted the birds to enter small spaces between the bark and tree trunks. Base materials, gathered one piece at a time and consisting of twigs and strips of bark, conformed to the size of the nesting crevice. Nest cups, lying to the center and on top of the base materials and consisting of finer materials gathered in tufts, conformed to the size of the bird. While the female birds collected materials for the nests, their mates sang close by.

Nest-building periods for two nests in this study were about six and seven days long.

Egg-laying began the morning after completion of the nest. The most common clutch size was six eggs (6 nests).

Females did all of the incubating during a total of 15 hours of recorded observations (8 nests). Females incubating six eggs arranged them in two rows of three, lengthwise. Attentive intervals varied widely. Males brought food to their two incubating mates. Females left the nest to receive the food. Two color-marked clutches had 15-day incubation periods.

Immediately after hatching, young creepers were blind and practically naked except for dark gray natal down on their heads. Eyes were open by Day 8. By Day 11, brown and white feathers and white wing bars were visible. By Day 12, nestlings began climbing briefly above the nest cups behind the bark scales. They poked their heads out of the nesting cavities for food.

Only females brooded young.

Both adults fed young soon after hatching. They mainly gleaned tree bark for insects and arachnids which they fed to one nestling per feeding trip.

Adults carried fecal sacs away from the nests to trees where, with one quick movement of the bill, each sac was slapped on the bark where it stuck.

Fledging occurred 15 to 16 days after hatching.

Family groups were always seen within approximately a 500-meter radius of their former nests. Frequently the birds separated in two distinct feeding groups; one fledgling group followed one parent, a second group followed the other. Between active feeding periods, young fledglings rested singly or in groups, pressing against the bark.

Fledglings roosted close together, forming a tight circular patch of birds. Adults did not join the night roost.

Fledgling and adult Brown Creepers pressed their bodies against the bark of a tree trunk when potentially dangerous situations (such as the scream of a hawk) developed in the nesting area.

Eleven (58%) of the 19 nests containing at least one egg or nestling succeeded in fledging young. Of a total of 94 eggs laid, 56 hatched, and 49 young fledged. There were no renesting attempts after a successful nesting. The fledgling success rate at Neithercut more closely approached Margaret Nice's calculation of egg-to-fledgling success for altricial open-nesters than it does for altricial hole-nesting species.

Nest loss occurred four times as a result of alteration of the bark scale due to rain or wind, once due to brood parasitism by a Brown-headed Cowbird, three times due to predation, and twice due to human disturbance.

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Dr. Olin Sewall Pettingill, Jr. inspired the study. Kathy Fahey and Leo Kretzner helped with the all-day nesting observations at the second nest found during the study. Dr. Nicholas Cuthbert provided advice in the preparation of the manuscript. Mr. George Pellerin and Dr. William Theunissen critically reviewed the manuscript. Terry Davis continually encouraged me when it seemed as if the right words would never come.

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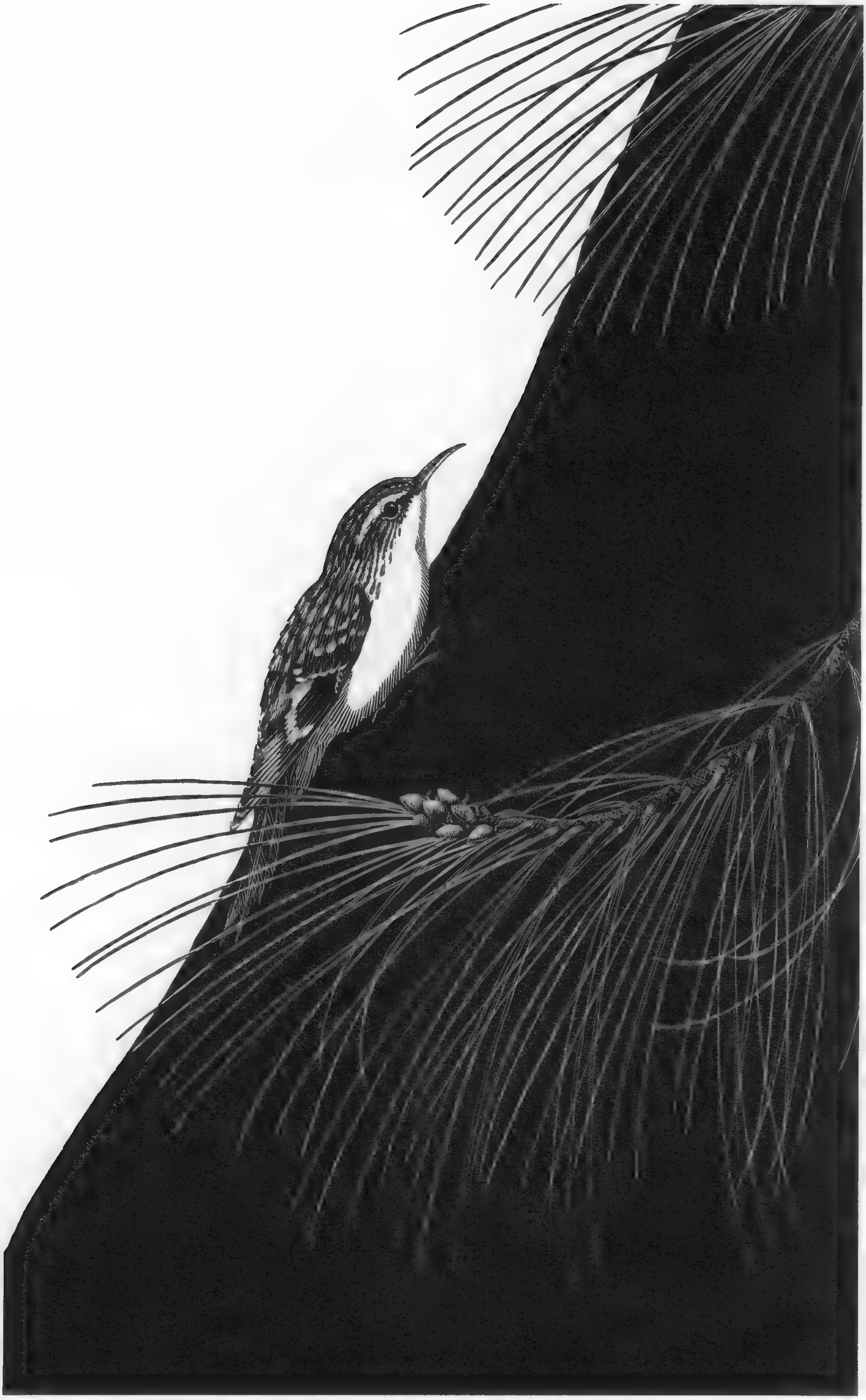

Brown Creeper, *Certhia familiaris*. Drawing by Dana Gardner.

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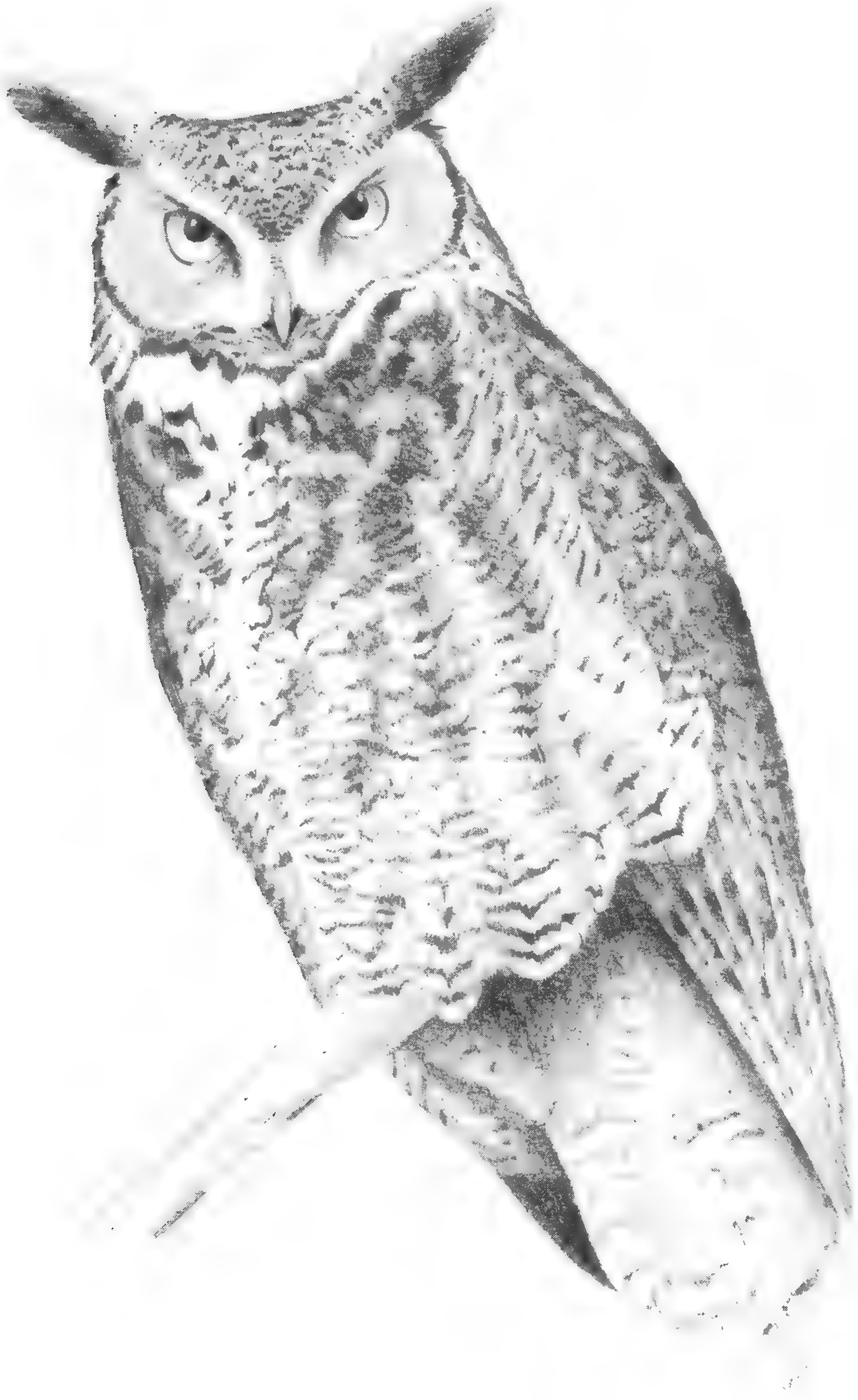

Great-horned Owl, *Bubo virginianus.* Drawing by Richard Casey.

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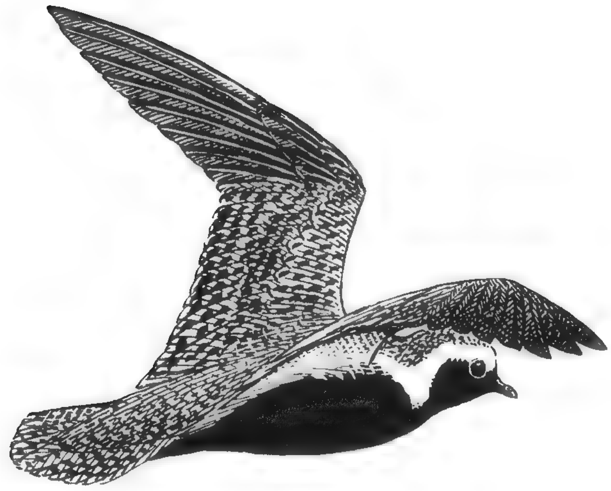

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CONTENTS

A YELLOW RAIL SKETCH. *George Miksch Sutton* 5

FORAGING AND COEXISTENCE OF SPRUCE-WOODS WARBLERS.
Douglass H. Morse 7

BEAUTY AND THE BEAST: NATURAL HISTORY AND ART.
Robert M. Mengel 27

COMPARATIVE ECOLOGY OF THE MOUNTAIN AND CALIFORNIA
QUAIL IN THE CARMEL VALLEY, CALIFORNIA. *Ralph J. Gutiérrez* 71

LIFE HISTORY OF THE FIVE-STRIPED SPARROW. *G. Scott Mills,*
James R. Silliman, Kathy D. Groschupf and *Steven M. Speich* 95

THE EVOLUTIONARY BIOLOGY OF KINGFISHERS (ALCEDINIDAE).
C. Hilary Fry 113

THE CONTRIBUTIONS OF THE AMATEUR TO NORTH AMERICAN
ORNITHOLOGY: A HISTORICAL PERSPECTIVE.
Marianne Ainley 161

GROUND BARBETS OF EAST AFRICA. *Lester L. Short* and
Jennifer F. M. Horne 179

SWINHOE'S PHEASANT IN TAIWAN. *Sheldon R. Severinghaus* 189

LE CONTE'S SARROW: A RARE STUDY FROM LIFE
Robert M. Mengel 211

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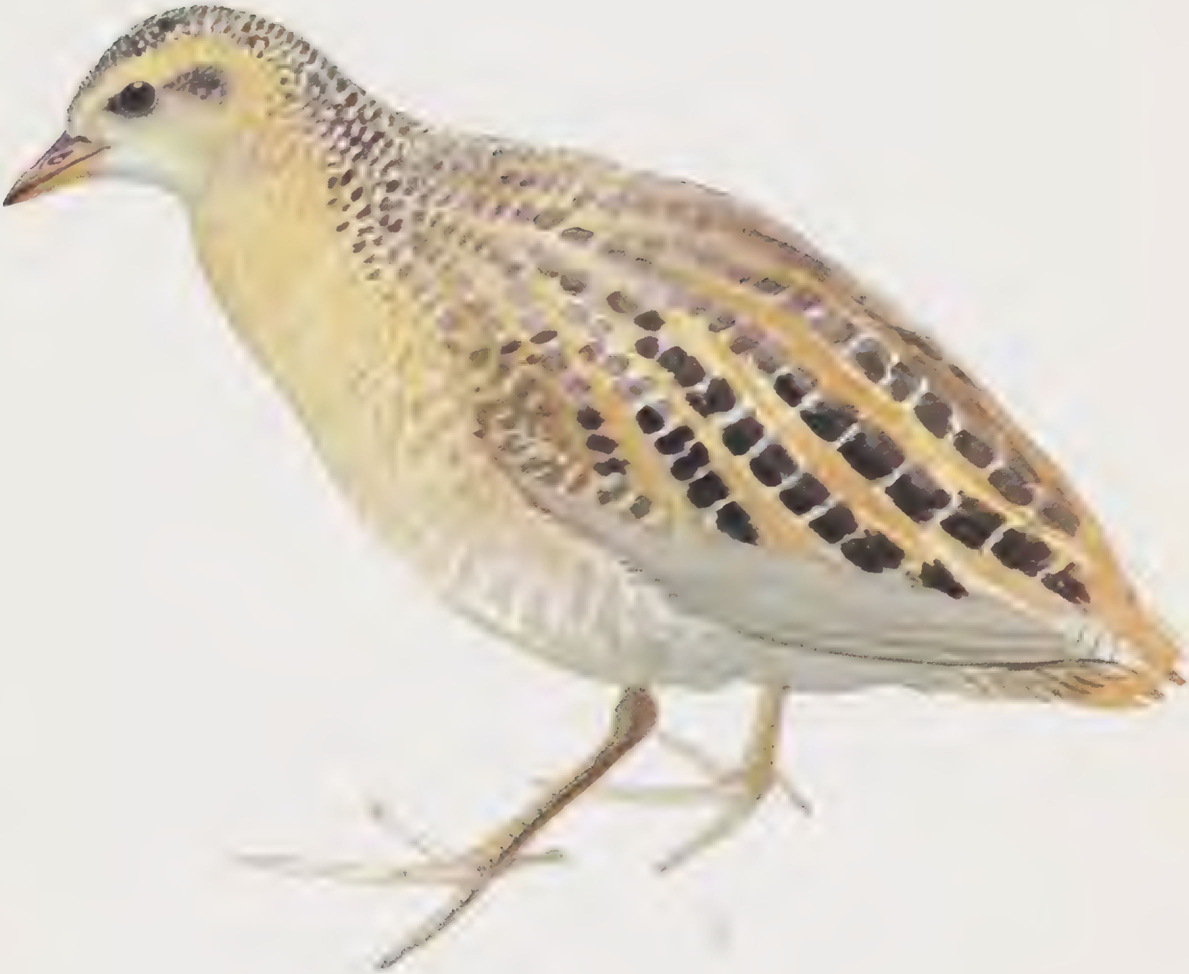

Yellow Rail, *Coturnicops noveboracensis*. Watercolor. Painted directly from life by George Miksch Sutton.

A YELLOW RAIL SKETCH

George Miksch Sutton

Most bird students will agree that the Yellow Rail *(Coturnicops noveboracensis)* is not often seen alive. The species is not found exclusively in wet areas difficult to walk through, but is so averse to being flushed from cover that it prefers being trod on to being seen at all—an important fact that I learned first-hand near Last Mountain Lake, southern Saskatchewan, in the summer of 1932. That summer W. E. Clyde Todd, Albert C. Lloyd, and I were making a study of the birds of that part of the great province.

On the prairie near the lake were circular patches of knee-high, spring-fed sedge whose green was of a lighter, more yellowish shade than that of the grass. These patches of not quite marshy habitat roused my interest, for whenever I walked across them I heard a metallic *tick-tick-tick* that could be matched to perfection by tapping a cartridge against the barrel of my 12-gauge shotgun. If I wanted to hear the cry, all I had to do was strike the gun's barrel rather rapidly three times, and listen. The answering *tick-tick-tick* came almost at once, sometimes only a few feet away. Since I failed to see anything like a katydid or flying grasshopper, I decided that the cry must come from a bird or mammal. When, on June 13, I chanced to see a small, short-tailed brown bird jump without spreading its wings for an insect high on a stem of sedge, I thought *rail* instantly. But which rail? Determined to find the answer to this question, I crossed and re-crossed the patches of sedge, neglecting other habitats. Failure; nothing but failure! I did learn, however, that the *tick-tick-tick* always came from the sedge, not from the grass.

Bert Lloyd suggested that we borrow a Springer spaniel from someone he knew in Davidson, his home town. The friendly dog, joyful over this chance to "do his thing," flushed a hen shoveller from her nest and yelped excitedly as he gave chase, paying no attention at all to shouted commands that he stop and come back. His job was to *get that duck*, and the duck, a faithful mother, feigned injury so successfully that she led her pursuer almost to the horizon. The poor dog, utterly done-in, had to be found before being taken home that evening.

Meanwhile the three of us, walking abreast without the dog, charged across the patches of sedge back and forth, back and forth, intent on scaring up what we could. Came the moment when Bert Lloyd saw what he thought might be a rodent, said something like "Could be a rat!" and lunged full-length in pursuit, winding up flat on the ground, surrounded by sedge.

Under him was . . . a Yellow Rail, the first any of us had ever seen alive. The little thing made no sound as it was extricated from the sedge, though it kicked energetically. It was an important capture: the first Yellow Rail for the province of Saskatchewan.

My second living Yellow Rail was brought to my office on the Cornell campus on 23 October 1937. It had been caught by some graduate students in a dry upland field well away from water. It was a charming little creature—slim, graceful, almost "cocky" in bearing, in this respect being unlike any rail I had ever watched. Kept in a small cage, it was a fine model, though it rarely stayed in one place very long at a stretch.

I do not recall what obliged me to leave my drawing long before it was finished. What I do recall is the almost frantic way in which I turned that office upside down trying to find the rail. It was not in the cage. Nor was it under or back of any case or in any drawer. It had simply evaporated.

My guess is that the students who had captured the bird decided to take matters into their own hands, to return the rail to the field in which they had found it, thus making sure that it would not be "collected" and skinned when I was through with the drawing. I cannot swear that this happened, of course. What I can swear is that the bird was no longer in my office when I returned to finish the sketch. Nowhere! Having been a graduate student myself once upon a time, I know how delicious the flavor of defying tradition can be. That little bird was not to become anybody's specimen: it would continue, praise the Lord, to be a living Yellow Rail!

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FORAGING AND COEXISTENCE OF SPRUCE-WOODS WARBLERS

DOUGLASS H. MORSE

The wood warblers (family Parulidae), small, foliage-gleaning, insectivores of the New World, include some of the most colorful of bird species. Not only do they rival tropical birds in their bright coloration, but they do so in their variety as well. The family consists of well above one hundred species distributed throughout almost all of temperate-zone North America and the New World tropics [*8*]. Most impressive, though, is the number of species that one may encounter at a single place at the same time. Wood warblers are notorious in this respect, for as many as 20 to 30 species may be found simultaneously at the height of the spring migration. Of greater interest to the ecologist is that several extremely similar species may breed side by side in the same forest. It is this aspect that I wish to pursue here, for it represents my major interest in this group for the last 15 years. I have worked primarily with the genus *Dendroica*, which has the most species of any northern genus in this family, and with the Northern Parula *(Parula americana)*. As many as four to six members of this genus may breed at the same time in a single spruce forest along the Maine coast. The late Robert MacArthur [*15*] studied them in the mid-1950's for this very reason. At that time they seemed to provide an exception to the competitive exclusion principle, which briefly states that no two species can coexist indefinitely if they use the same resources and if those resources are limiting their density. Ecologists now know much more about assemblages of similar species than they did 25 years ago, in part the result of work with these very birds, but at that time it was unclear how there could be so many "peas in a pod."

How the Similar Species Coexist

Consider the situation: in a single mature, undisturbed spruce forest one can find five or more species of these warblers living together during the breeding season. Given the apparent homogeneity of such a forest, it was not immediately evident how these birds coexisted on a site unless they were violating the competitive exclusion principle. Looking a little more carefully at the principle as stated, several possible explanations become apparent. The situation observed might be temporary, in which one species is in the process of crowding out the others. Alternatively, resources might not be limiting. Instead, predators or climatic factors, such as weather, might be controlling their numbers to the point that more than adequate food, nest-sites, and other needs exist to go around. Lastly, these species might not be using the same resources.

We now know that the last alternative accounts in large part for the presence of several species of warblers together. The relationship between them is not temporary, at least for many of the species, and resources do appear potentially to be limiting at times. The birds "view" the forest on a rather different scale than we do. In MacArthur's study, five species of warblers partitioned this forest into five sub-forests, with each species concentrating its activities in a discrete part by varying the height and/or distance from the trunk at which they foraged (Figure 1). To be sure, overlap occurred among the species; in fact, if one watches a Blackburnian Warbler *(D. fusca)*, normally a treetop forager, long enough one may see it feeding on the ground. Similarly, the Yellow-rumped (Myrtle) Warbler *(D. coronata)*, while normally a denizen of the lower parts of the forest, can occasionally be observed foraging in the tops of trees. However, each of the species differs markedly from the others in a quantitative sense, having its own area of specialization (Figure 1). Therefore, the competitive exclusion principle received strong support, and concurrently new insight was obtained on the precision with which potentially competing species might partition themselves.

Important as MacArthur's study was in developing thinking in a large area of ecology, it did not address itself to several other important questions. For instance, while it established conclusively that niche partitioning might occur among similar species in a homogeneous, if complex, habitat, it said little about how that partitioning might take place; that is to say, what the rules of assemblage were by which this relationship was maintained. This has been an abiding interest in my investigations.

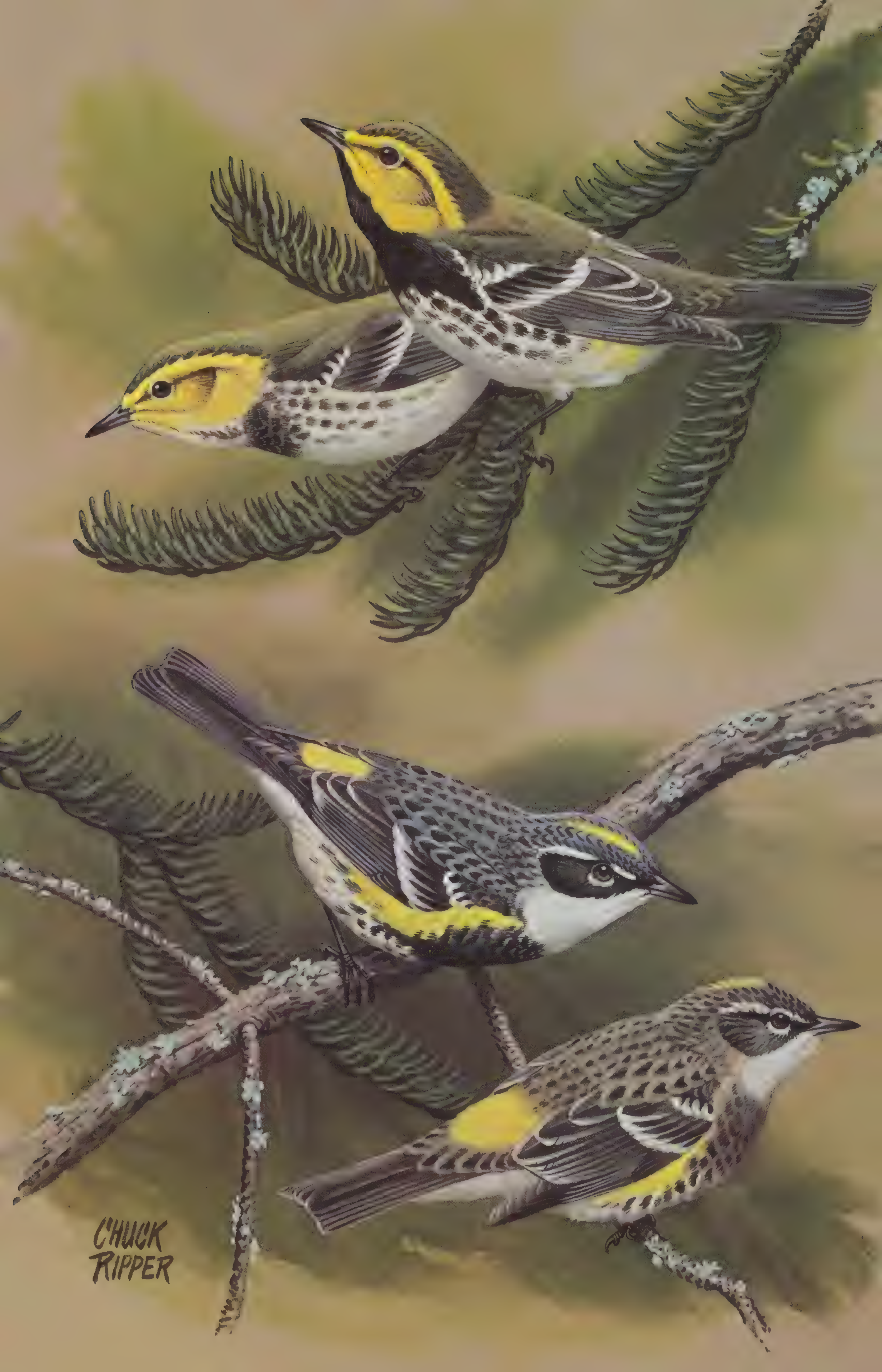
In the early 1960's I had an opportunity to study a similar assemblage of *Dendroica* warblers in another spruce forest along the Maine coast, about 100 kilometers west of MacArthur's study area on Mt. Desert Island. I quickly determined that the basic pattern reported by MacArthur [*15*] applied to the warblers in my forest as well, even though the species composition (Figure 1) differed slightly here [*21, 22*]. I was also struck by the potential that these birds offered for further studies of relationships between species. Several questions immediately presented themselves: What is the individual variation among the birds present? For instance, do males and females of a given species partition their habitat in the same way that two sympatric species do? By what means do the different species manage to keep separated? Why was the species composition in my study area different from that of MacArthur's, some 100 km to the east? Why are there usually so many more species of *Dendroica* warblers in this habitat than in most others? On this last point, only a single species of *Dendroica*, the Pine Warbler *(D. pinus)*, usually occupies the loblolly and longleaf pine forests of the southeastern United States [*6*].

Sexual Differences in the Use of Resources

I soon discovered that the males and females of each species foraged in different places [*22*]. Therefore, the picture was actually more complicated than MacArthur had suggested; one might say that instead of four species here, I essentially had eight. What is the basis for this intersexual difference, and what is its importance to the real foraging diversity attained within the community?

The partitioning has a rather simple basis: males forage higher in the trees than do their females. However, they both use the same structural parts

Black-throated Green Warbler (above; male, right) and Yellow-rumped Warbler (below; male, left). Painting by Chuck Ripper.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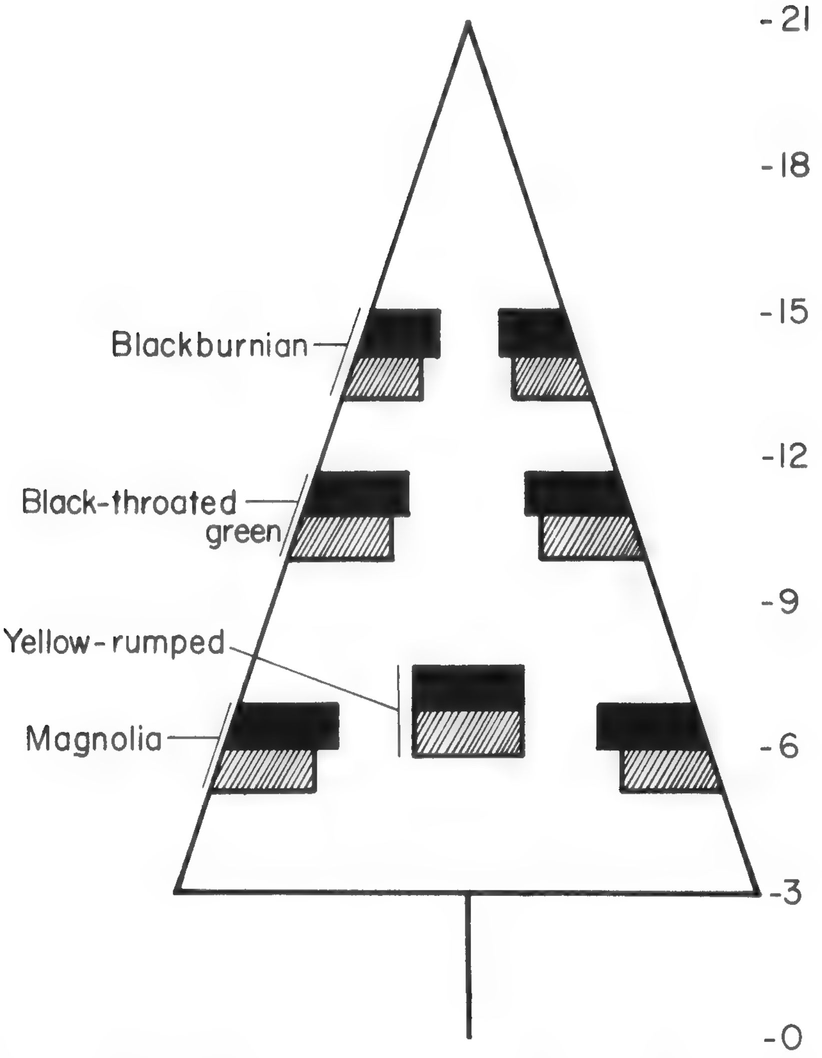


Figure 1. Centers of foraging areas of spruce-woods warblers in Maine. Solid color represents males; hatched represents females. Numbers on the right represent height in meters. Data from Morse 1967 and 1968.

of the foliage (Figure 1). For example, although male Black-throated Green Warblers *(D. virens)* forage higher than do their females, both exploit the inner and outer parts of the foliage, whatever the height, with similar frequency. Since the same pattern holds for each of the four species that I explored, this suggests a common thread.

Male Role

The common thread seems to be that the two sexes have markedly different duties associated with the reproductive effort. These species are all intensely territorial, at least intraspecifically; and in these dense populations the males spend much of the time defending their areas from others. Much of this defense is highly ritualized, and after the territories are set up early in the season, physical contact (Figure 2) between males declines rapidly [*28*]. Song, and probably associated visual display, apparently substitutes for overt physical efforts. Thus, relatively long-range communication has, in part, taken the place of fighting [*23*]. These displays may succeed in detracting males from invading neighboring territories, as has been shown in certain other species of songbirds [*7, 12*]. Effective long-range communication to individuals on adjacent territories is best carried out in locations from which the signals can be effectively broadcast. Not surprisingly, much of this singing takes place in exposed positions, particularly ones at fairly high elevations [*21*]. Given that much of their time is taken up displaying at relatively great heights in the foliage, it is not surprising that the males should forage there also.

Female Role

The entire responsibility of incubating the eggs and probably feeding the newly-hatched young as well falls to the females. Nests are typically placed at considerably lower elevations than the singing perches, which diminishes their exposure (storms may at times be severe). It may also result in their being less conspicuous to predators than they would be otherwise. For purposes of efficiency alone, it seems reasonable that the females would forage at the same general level as their nests. Efficiency of foraging may be at a premium for females at this time. It gives them access to a food source (insects) near the nest that is not heavily picked over by the male. The female may be considerably stressed at this time, for she spends at least 85 percent of her time incubating eggs. When she does leave the nest, she forages at an

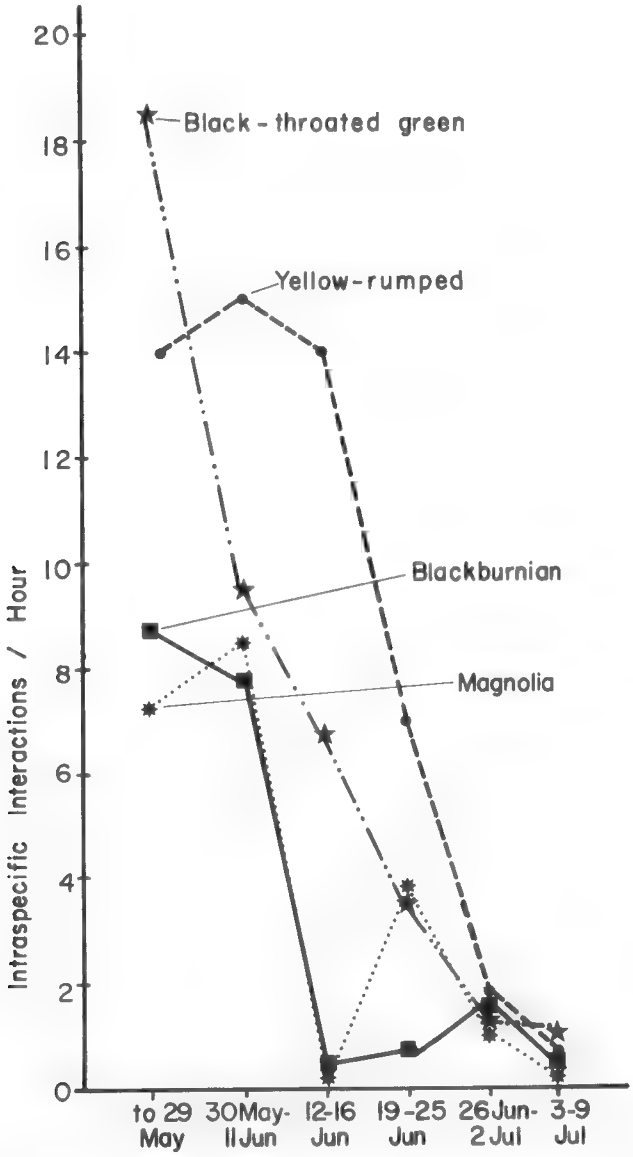


Figure 2. Frequency of intraspecific chases, fights, and supplanting actions of spruce-woods warblers in the breeding season. Data from Morse 1976a.

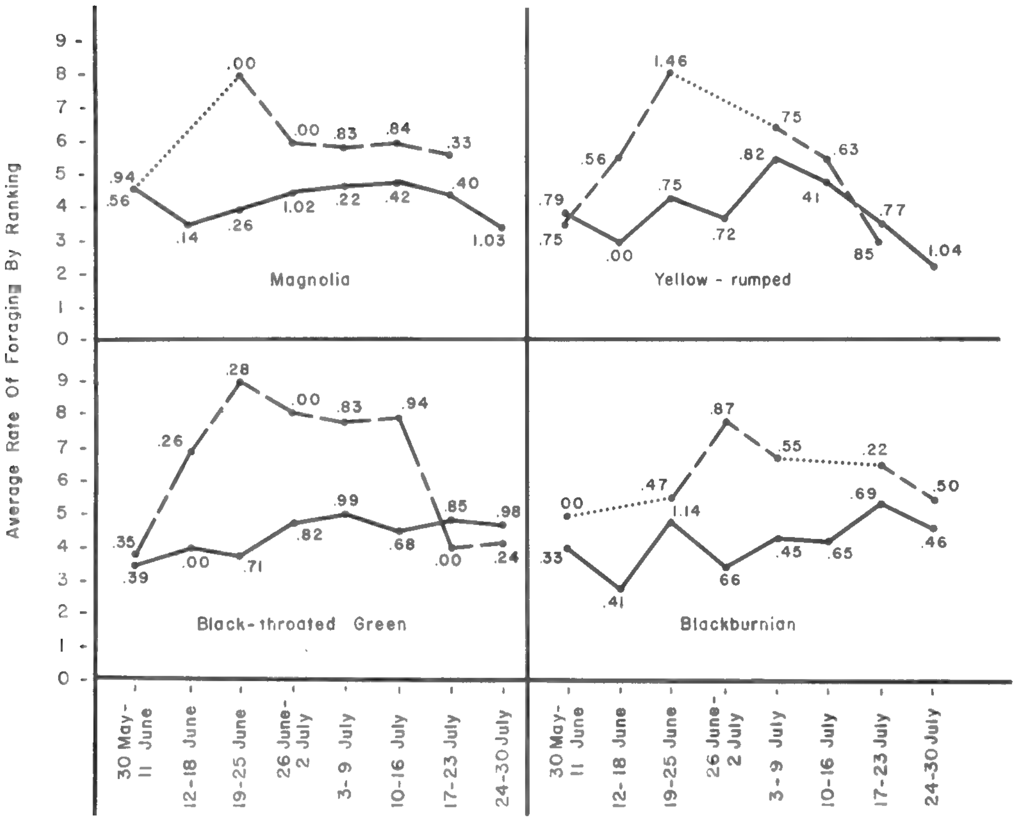


Figure 3. Mean foraging rates of male (solid lines) and female (dashed lines) warblers over a season. Almost without exception males foraged more rapidly than females. Each number accompanying a point in a graph is one standard deviation. Dotted lines in the graphs connect two points that flank a missing data point. Rate of foraging refers to the number of foraging motions (gleaning, hovering, hawking for insects, etc.) performed per minute. Rank 1 = 1–2 foraging motions/minute; Rank 2 = 3–4 motions; Rank 3 = 5–6 motions; Rank 4 = 7–9 motions; Rank 5 = 10–12 motions; Rank 6 = 13–15 motions; Rank 7 = 16–20 motions; Rank 8 = 21–25 motions; Rank 9 = 26–30 motions; Rank 10 = over 30 motions. Modified from Morse 1968.

extremely rapid rate (Figure 3), far faster than the male and faster than her actions at other time [*22*]. One could argue that, were it not for the presence of this undiluted food supply, she would be unable to tend the eggs by herself.

An Explanation for the Dichotomous Roles

Why doesn't the male help out with the incubation process, rather than go his own way? I have already suggested that constant display is of great importance in defending the territory; furthermore, there is the added chance that the male might attract predators to the nest by virtue of his somewhat brighter coloration. At present it is impossible to distinguish between the two alternatives, but perhaps both are acting simultaneously. It is not uncommon for female songbirds to perform most or all of the incubation; however, the contribution of the male about the nest may often be greater than occurs in these warblers. For instance, a male Yellow Warbler *(D. petechia)* living in shrubby areas may feed his incubating female on the nest [*20*], thus alleviating some of her energetic difficulties while she adheres to a tight activity budget. However, the male spruce-woods warblers do not regularly assist in a similar way. A likely reason lies in the relatively high vulnerability to nest predators in the spruce forests, where both red squirrels *(Tamiasciurus hudsonicus)* and Blue Jays *(Cyanocitta cristata)* are constant threats. Slipping off the nest quickly and silently for minimal periods of time may represent an effective way of minimizing nest predation [*29*]. While incubating, both the female and her nest are inconspicuous, given the striped back of the female and the construction of the nest from twigs. Thus, the male-female partitioning seems an excellent compromise to accommodate the varying contingencies presented by both food-gathering and predator-avoidance pressure.

Interspecific Partitioning in Other Species

What does this imply about the remarkable pattern of interspecific partitioning seen in this forest, however? Earlier I suggested that when females forage differently from males, it is the ecological equivalent of doubling the number of species. The pattern of between-sex partitioning might thus seem more likely in a community with few similar species than in one with many. In fact, this type of partitioning is known to occur with relative frequency on islands with only a few species [*34*]. Certain advantages might exist even in more diverse communities, however. This partitioning should permit highly efficient patterns of exploitation. Not only might both sexes be able to specialize, but if the separation is spatial, a given individual might be able to regulate precisely its foraging activities within a relatively small area not heavily exploited by its mate. It could thus return to the area it has most recently hunted, with a high probability that a given resource it has begun to exploit may still be there. It can, by exploiting a small area, also avoid areas that are not productive. Zach and Falls [*39*] have shown, in fact, that another warbler, the Ovenbird *(Seiurus aurocapillus)*, probably does avoid areas which it has recently exhausted or that are otherwise largely devoid of food. Since the major difference in foraging between the two sexes is in height above ground, male and female occupy somewhat different feeding spaces, even though differences in techniques of exploitation do not

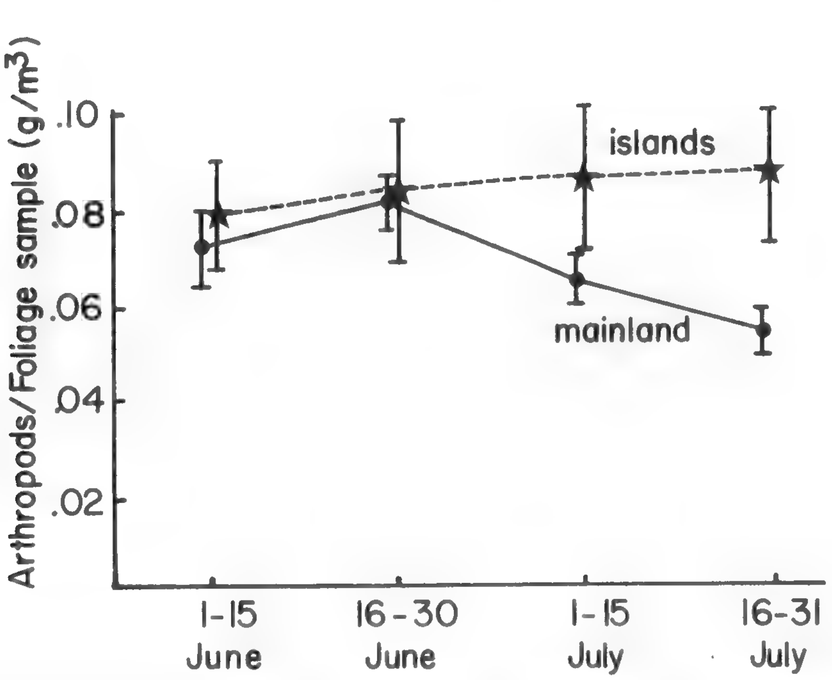


Figure 4. Biomass of insects and other arthropods collected from samples of spruce foliage at mainland and island study areas. Horizontal bars represent one standard error of the mean. Modified from Morse 1976b, 1977.

differ appreciably. Other experimental studies on the foraging of songbirds [*13, 14, 36, 37*] suggest that members of this group regularly follow rules as precise as those suggested for the male and female spruce-woods warblers.

A system whereby each sex forages in different areas, such as I have described, should depend upon a rich and predictable food supply. Sampling studies of the insect supply (Figure 4) suggest a rather rich resource base for the birds during most of the season [*29*]. However, these data were gathered from dry foliage and do not adequately reflect the availability of these items during extended rainy spells. Both inactivity of insects and the danger of thoroughly wetting the plumage may make foraging very unprofitable at such times. It is during these periods that most abandonment of eggs or young occurs [*25*]. The quality of the females' foraging area may be most critical at this time. While she might potentially invade the male's domain under severe conditions, it is her own area that is likely to be most protected from exposure to rain and fog, so that it should remain the most profitable place in which to forage.

What Happens When Fewer Species Occur Together?

Would these species use exactly the same techniques if one or more of them were not present? An answer to this question might help to explain why several species coexist, rather than one species replacing the rest. After all, even though the warblers are clearly treating different parts of the trees as distinct resources, the types of actions that they perform in exploiting these trees for their insects and nesting materials and sites all require broadly similar capabilities and movements.

Most workers interested in this problem have compared isolated populations of individuals, such as ones on islands, with their relatives that live on the more species-diverse mainland. For instance, Crowell [*5*], and Sheppard, Klopfer, and Oelke [*35*], compared the resident land birds on Bermuda with members of the same species on the adjacent North American mainland. These efforts provided considerable insight into the problem; however, they cannot answer one important question: how much have the gene pools on Bermuda diverged from those on the North American mainland? Island populations of animals and plants often accommodate rather rapidly to the conditions on the islands [*4*], which may result from a different composition of competitors or predators, or from differences in the habitats on the islands. All of these factors could rather quickly make these birds quite different from their mainland relatives. Certain Bermudan populations have even differentiated to the point that they have been accorded subspecific status [*1*]. If their morphology has changed that much, it is possible that their behavioral repertoire may have changed as well. If so, it is impossible to separate differences that have evolved in isolation and characteristics that may exist within the repertoire of mainland birds but that are seldom exhibited because of the restrictions typically imposed upon them by other species. It usually seems to have been implicitly assumed that differences between island and mainland are of the latter type, but no compelling basis exists for this assumption.

The Nature of Habitat Partitioning

The spruce-woods warblers provide an excellent opportunity to investigate the nature of partitioning. Several tiny islands lying immediately adjacent (200 m to 1.5 km) to the primary study areas (Figure 5) provide natural experiments, for by choosing islands of different sizes one can obtain different combinations of these warblers. Three species of spruce-woods warblers, the Northern Parula, Yellow-rumped, and Black-throated Green, commonly nest on them. The genus *Parula* is closely related to *Dendroica*. These individuals are part of the same population as those in the surrounding large forests; in fact, on two occasions I have witnessed apparent occupation of these islands by birds flying from the mainland [*25*].

The order of colonization of these islands is extremely predictable. Almost invariably, if only one species is present, it is the Northern Parula; if two species are present, they are the Northern Parula and the Yellow-rumped Warbler; and Black-throated Green Warblers are only present if the other two species are as well. Looking at their overall pattern of resource exploitation on these islands, the Northern Parula and Yellow-rumped Warbler expand their areas of resource use both vertically and laterally, while the Black-throated Green Warbler does not (Figure 6). The picture is even more striking when one compares the territory sizes of the three species on the small islands and on the mainland. The Northern Parula and Yellow-rumped Warbler, the species showing a shift in resource exploitation, also occupied much smaller territories on the islands than they did on the mainland (Figure 7). No such trend occurred in the Black-throated Green Warbler, the species that did not change its niche dimensions. Apparently, by foraging more broadly within an area, the Northern Parula and Yellow-rumped Warbler can exist in a smaller territory; hence, they have occupied islands much smaller than would be predicted on the basis of the mainland

Figure 5. A representative small island used in the study. This island usually supported Black-throated Green and Yellow-rumped Warblers and Northern Parulas.

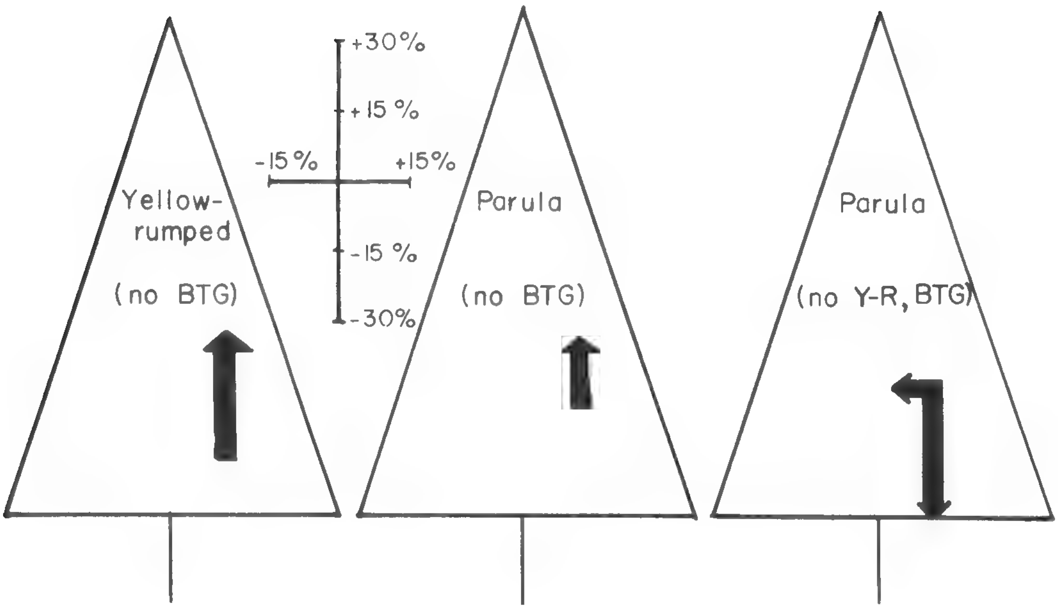


Figure 6. Expansion of foraging ranges of the Northern Parula and Yellow-rumped Warbler on small islands when other warblers were absent. The left dendrogram illustrates foraging shifts of Yellow-rumped Warblers when no Black-throated Green Warblers were present; only Northern Parulas were present. The center dendrogram illustrates foraging shifts of Northern Parulas when no Black-throated Green Warblers were present; only Yellow-rumped Warblers were present. The right dendrogram illustrates foraging shifts of Northern Parulas when neither Yellow-rumped nor Black-throated Green Warblers were present; no other spruce-woods warblers were present. The direction and length of the arrows in the dendrograms indicate the direction and magnitude of the foraging shifts (higher or lower, inward or outward) in the trees. Data from Morse 1971a.

data alone [*30*]. The food supplies on the mainland and islands are similar [*30*], thus precluding the likelihood that this factor is responsible for the differences (Figure 4).

What might account for these differences between the warblers? The failure of one species to change implies that it is already exploiting a situation that is optimal for it, at least in relation to its interactions with the other species. Calculation of the social dominance relationships of the different warblers—that is, the ability of one kind to displace another where some resource is being contested—showed that the Black-throated Green Warbler, the species that did not change, was the socially dominant one [*28*]. The Black-throated Green Warbler, therefore, was not in danger of being displaced from resources by the other warblers on the tiny islands, though they might exploit such resources in its absence. That the other two warblers apparently were under such restraints is suggested by their position in the hierarchies and by their expanded foraging activities when their dominants were absent.

Thus, it appears that relationships among these three species in the large community are dynamic, and that they are strongly structured by the relatively inflexible Black-throated Green Warbler. If the size of the different species' breeding populations are determined by the number of territories they can occupy, the results from the island-mainland comparisons suggest that the socially dominant Black-throated Green Warbler may in effect be strongly influencing the size of the other species' breeding populations, and hence, the quantitative makeup of the community [*27*].

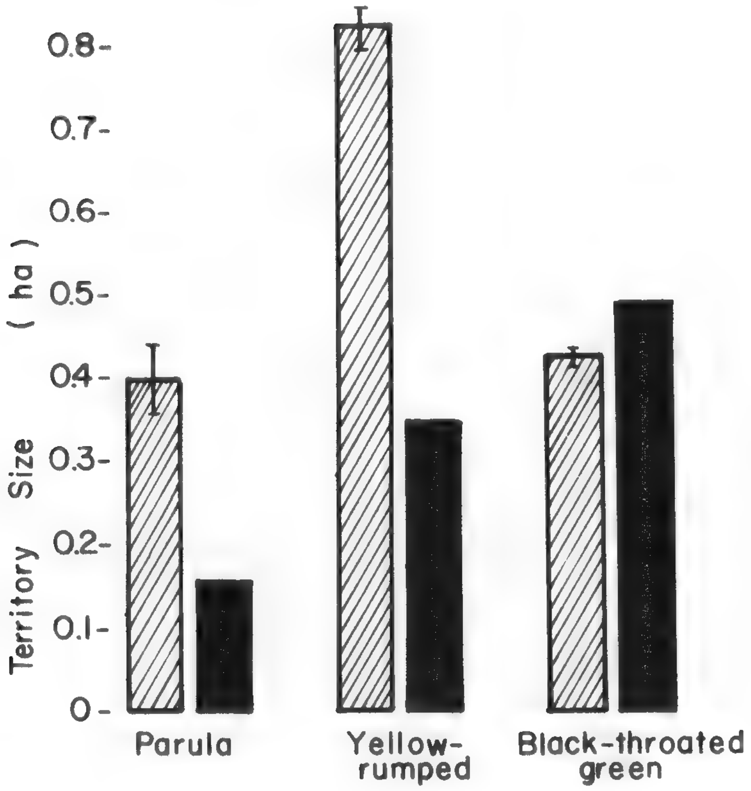


Figure 7. Territory size of spruce-woods warblers on mainland study areas with one standard error of the mean (hatched bars) and territory size of the same species on the smallest island occupied by them (solid bars).On the smallest islands it is assumed that the entire forested areas were occupied by the warblers. Data from Morse 1977.

Changes in Population Density

There is some evidence for this very possibility. First, breeding densities of these birds may be extremely constant over considerable periods, even several years at a time [*29*]. However, catastrophic years when few young are reared may so deplete the population size that an inadequate number of individuals remains to maintain the previous breeding density. Such conditions apparently followed the rainy and foggy summers of 1972 and 1973. The numbers of spruce-forest warblers on the tiny islands then sank to their lowest level in the 10 years of monitoring them (Figure 8). Concurrently, Yellow Warblers and American Redstarts *(Setophaga ruticilla)*, species that had previously nested sporadically in these areas, increased significantly [*30*]. Why their numbers were not similarly affected is unclear; but since they normally occupy somewhat more open habitats than do the spruce-forest species, conditions may have been better for them during these years than they were in the wetter, often fog-shrouded areas on the islands and the edge of the shore. Regardless of its basis, the increase of these deciduous-edge species at the time that the spruce-woods warblers declined, strongly suggests that the presence of the latter had previously prevented the Northern Yellowthroat, Yellow Warbler, and American Redstart from attaining greater numbers.

The Black-throated Green Warbler also decreased markedly in some mainland forests. Coincident with its drop in numbers, Yellow-rumped Warblers increased. Possibly these extra individuals were recruited from marginal areas, such as the small islands. Given the relative inflexibility of the

Black-throated Green Warbler, it is not surprising that its numbers were most strongly affected under these conditions.

The decrease in numbers accompanying this climatic fluctuation provides strong evidence that this system is a dynamic one. Changes in the dominant and most important element, the Black-throated Green Warbler, may cause detectable adjustments in species and density compositions. Retention of flexibility is thus advantageous, and not simply an artifact of being accidentally situated on a tiny island, whose inhabitants make up only a fraction of one percent of the local population. This explanation does not totally account for the apparent lack of flexibility of the dominant Black-throated Green Warbler, and the relationship between social dominance and stereotypy requires further attention.

Black-throated Green Warblers Elsewhere

The pattern of resource exploitation described for the Black-throated Green Warbler here could not be maintained in some of its other populations. Although detailed descriptions of foraging have not been published from many other parts of its range, the habitats known to be occupied from

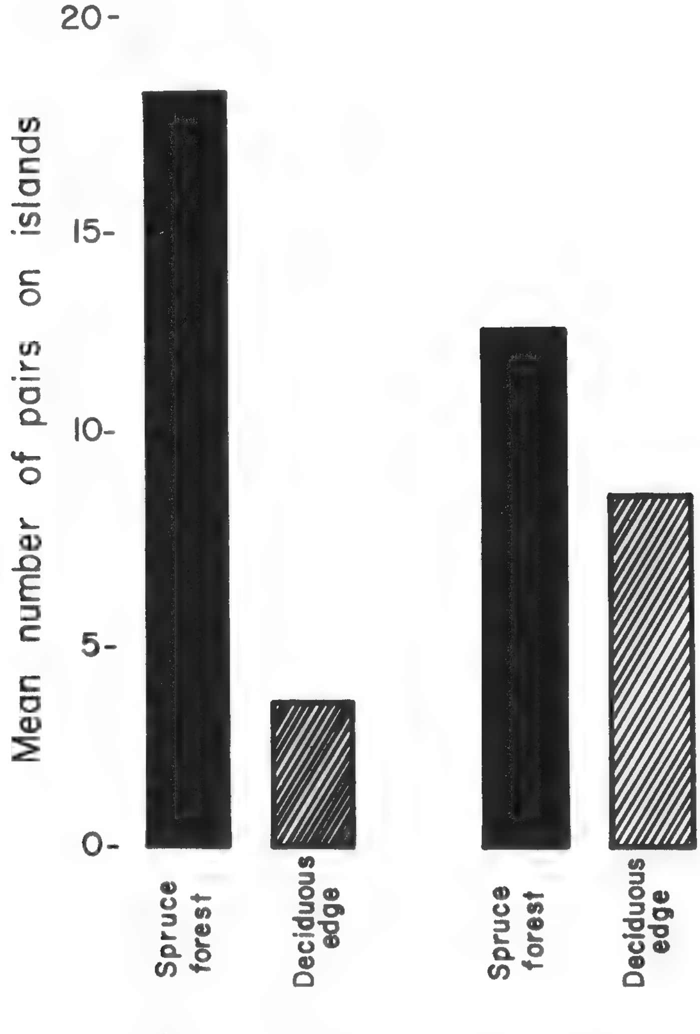
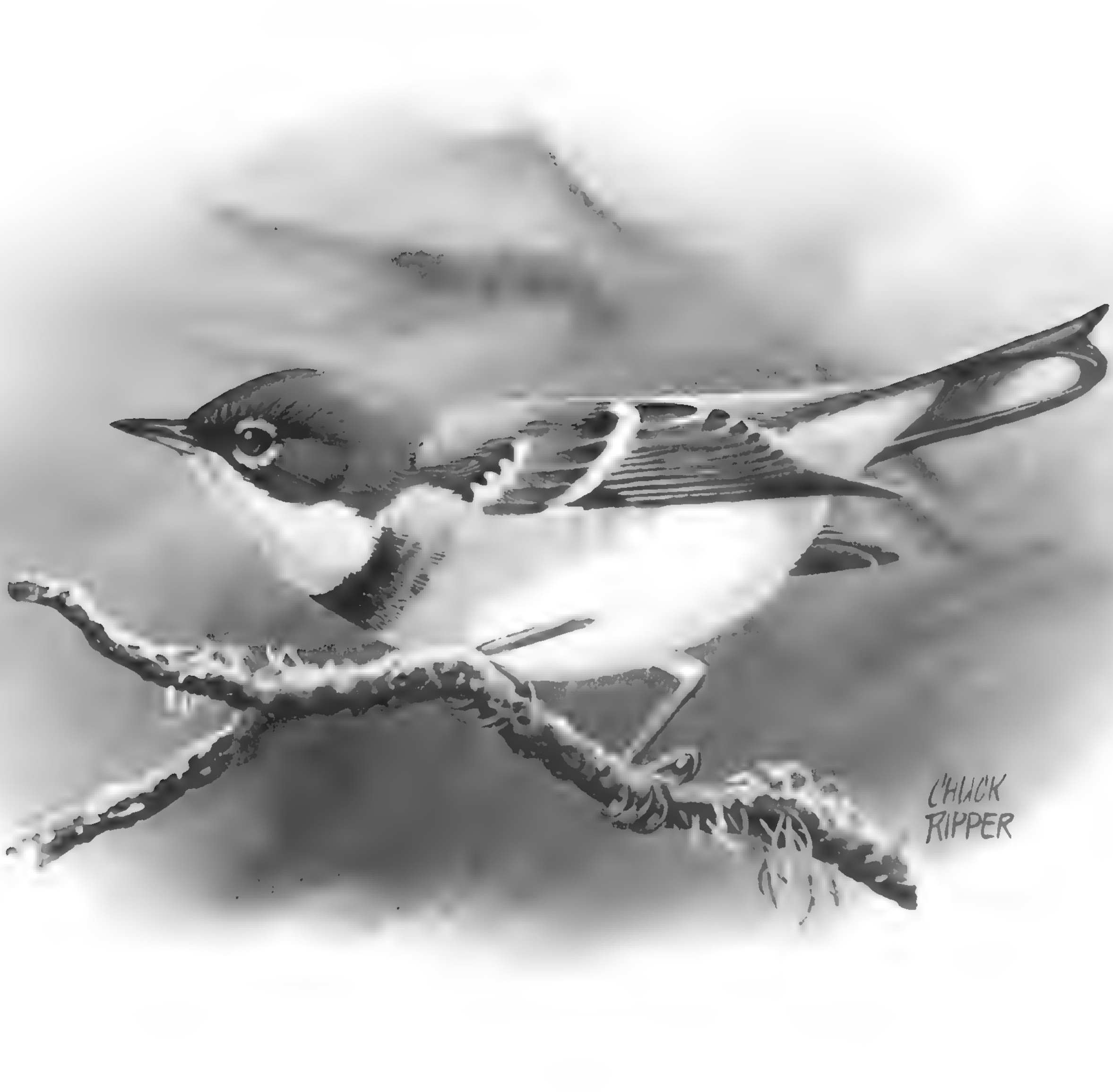


Figure 8. Change in density of spruce-woods warblers and deciduous-woods warblers on small islands. Warblers in the spruce habitat include Black-throated Green, Northern Parula, and Yellow-rumped. Warblers in the deciduous-edge habitat include the Yellow, American Redstart, and Northern Yellowthroat. Data from Morse 1977.

general accounts [*2, 8*] dictate that differences exist. For instance, in much of its extensive range along the Appalachian Mountain chain, this warbler occurs regularly in pure or nearly pure deciduous forest. In some places, such as in the Monongahela National Forest of West Virginia, it may be found on the mountainsides in a continuous gradient from spruce forests on the top to pure deciduous forests below. Rabenold [*33*] reported a broader range of foraging activities by this warbler in spruce forests of the southern Appalachian Mountains than in Maine. The overall patterns exhibited by the population that I studied along the Maine coast do not suggest a comparable flexibility in habitat choice, although at times the Maine individuals use birch trees that may occur within their largely coniferous territories. Birds immediately inland from my study areas may use pine or hemlock trees predominately in mixed coniferous-deciduous forests. In the Aroostock River Valley of northern Maine, Black-throated Green Warblers are uncommon in spruce-fir forests, the habitat most closely resembling their habitat along the Maine coast. Along this valley they occur regularly only in upland, mixed coniferous-deciduous forests, and then at only modest densities [*15, 31*]. Even this superficial glimpse indicates that tantalizing diversity must exist in the resource-usage patterns of this species, notwithstanding its rather stereotyped behavior along the Maine coast. Intensive studies of how different populations and different parts of a single population (perhaps along an environmental gradient) respond to keep variables, such as competitive regimes or environmental factors, should provide an excellent method for obtaining a better understanding of how resource exploitation patterns evolve.

Other Spruce-woods Warblers

Robert MacArthur's study included two additional *Dendroica* warblers, the Cape May *(D. tigrina)* and Bay-breasted Warblers *(D. castanea)*. These two species often concentrate their activities upon infestations of the spruce budworm *(Choristoneura fumiferana* Clem.), the larva of a small moth that periodically devastates spruce-fir forests in the northern United States and adjacent Canada [*18*]. In contrast to the usually stable populations of the species discussed up to now, Cape May and Bay-breasted Warblers often become abundant in areas of outbreaks, only to decline or disappear a few years after the infestation [*11*]. For this reason these birds have been the subject of considerable interest, partly in anticipation that they might be significant agents of biological control. It is now generally agreed, however, that these warblers have an insignificant effect on the budworms when the latter are abundant, although they may slow down or prevent prospective outbreaks when the pest's population densities are low [*18*]. If the Cape May and Bay-breasted Warblers only appear in numbers after a substantial increase of the budworm has commenced, it seems unlikely that they are responding soon enough to provide a measurable benefit to the trees, althoughout they are responding in a way that is propitious for their own welfare. When I studied these birds along the Aroostook River in northern Maine during June 1976, their densities—about one pair in every one-half hectare for the Bay-breasted Warbler and one pair in every four hectares for the Cape May Warbler—and those of the other insectivorous birds were at a level that would permit them to consume about one to six percent or the estimated 1.5 to 4.5 million budworm larvae and pupae present per hectare [*17*]. Furthermore, this infestation was not as severe as some [*31*], in which


CHUCK RIPPER

Northern Parula, *Parula americana*. Drawing by Chuck Ripper.

densities of budworms reached several times the density recorded here [*19*].

Cape May and Bay-breasted Warblers do not occur in many so-called equilibrium communities. They are not present at this time in the spruce forests along the coast of central Maine, where I have conducted most of my studies, although they were present in the 1930's in some of the very study areas that I used over the past 15 years [*3*]. Presumably they cannot compete successfully with the other warblers under equilibrium conditions, although several workers have reported that the numbers of some "permanent" species decrease at the time that numbers of Bay-breasted and Cape May Warblers peak. This decline could result from interference on the part of large numbers of the budworm specialists, or it could be a direct result of the budworms depressing the permanent species' normal insect supply, possibly through competition for vegetable food or destruction of hiding or oviposition locations of other insects. Implicit in the second alternative is the reasonable, but largely untested, assumption that the budworm specialists could prosper on a relatively monotonous diet, while the others could not. Some preliminary observations on aviary birds suggest that this is the case [*26*], but to the best of my knowledge no one has explored these alternatives thoroughly.

Why Are There So Many Sympatric Congeners?

Several features of this system probably account for more warblers of the genus *Dendroica* nesting here in Maine than in coniferous forests elsewhere or in rich deciduous forests.

The amount of food available in the spruce forests during the summer apparently far exceeds that of the southern hard pine forests (loblolly and longleaf pines), and is higher than that of most other coniferous forests as well [*6*]. Pulses of superabundant resources in spruce forests temporarily swell the species count further, and may largely account for the differences in warblers present in MacArthur's area and in mine. In the southern pine forests in particular, the high resin content of the trees apparently eliminates most kinds of insects, with the end result that only an extremely depauperate fauna is able to exist there [*38*]. It is not coincidental that these same forests are exploited for their turpentine and tar.

The foliage of eastern deciduous forests tends to be rather open and strongly lighted [*9*], with the result that dense foliage and shade are much less available than in spruce forests. While the number of bird species in many deciduous forests may exceed that of spruce forests, the number of extremely similar foliage gleaners is smaller [*16*]. Different species of spruce-woods warblers are specialized for foraging both on the inner and outer parts of tree limbs. On the other hand, the opportunities in spruce forests for capturing flying insects within or below the canopy are limited because of the small amount of open space. Rather than supporting a species of flycatcher, as is often the case in deciduous forests, spruce forests support other birds, such as Yellow-rumped Warblers, which combine gleaning with fly-catching.

In spite of the homogeneity of form in spruce forests, different heights do present different patterns of vegetational structure. The concentration of different species within parts of the habitat they use most frequently is closely associated with particular patterns of foraging, such as hawking for insects, hovering and gleaning. Densities of the different species appear to match well with the amount of vegetation present where they specialize; for instance, the Black-throated Green Warbler forages in an area of foliage that is two to three times greater in volume per unit area than that where the Blackburnian Warbler forages, and correspondingly it has a population density that often closely coincides [*21*]. What is particularly clear is that the relationships among these species are dynamic and fluid, such that, when one species declines or disappears, the remaining ones may occupy the vacated space to varying degrees. This pattern might be predicted, since the changes between the different "niches" are gradual rather than abrupt.

The explanation for the presence of this large number of similar *Dendroica* warblers has thus far escaped prediction by the simplest models, such as the relationship of the diversity of bird species to the diversity of foliage height found in many deciduous and grassland habitats [*16*]. Parenthetically, bird species diversity is a measure incorporating the number of species present and their relative abundance; foliage height diversity similarly incorporates the amount and relative abundance of vegetation at different

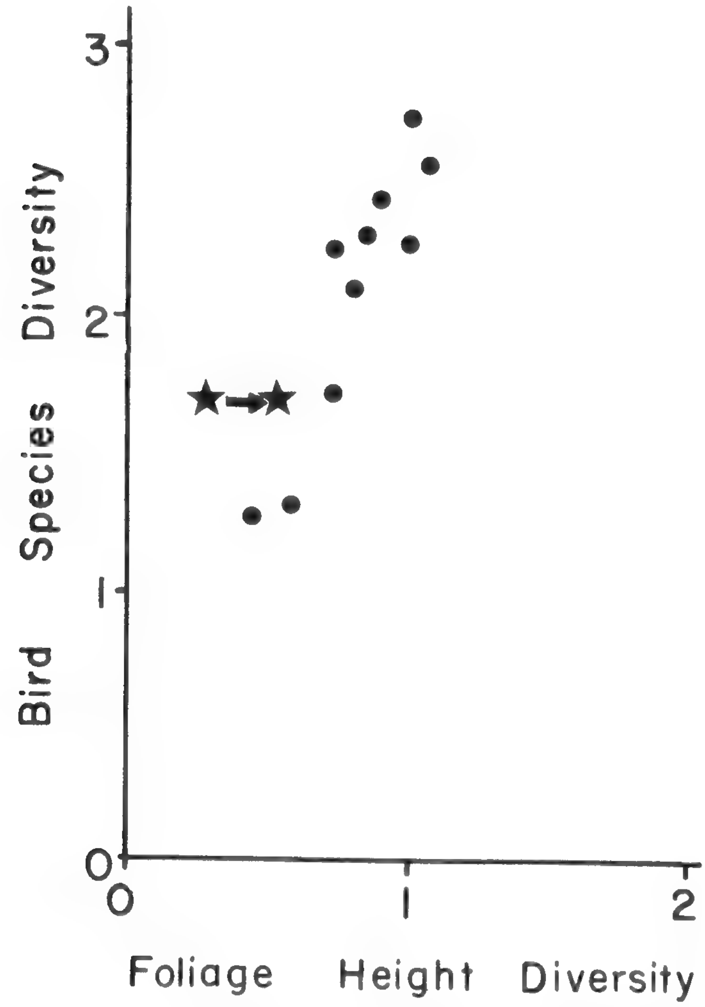


Figure 9. Relationship between birds species diversity and foliage height diversity, modified from MacArthur and MacArthur 1961. The left-hand star represents the position of MacArthur's spruce forest in his calculations, while the right-hand star represents the position of his forest if foliage height diversity is doubled, which would agree with the ability of spruce-woods warblers to partition the trees into inner and outer parts. This would put the spruce forest along the regression line of the other habitats shown in the figure, which represent deciduous forest and grasslands. Bird species diversity is calculated by the formula—$\Sigma\ p_i \log p_i$, where p_i is the proportion of all individuals belonging to the ith species. Foliage height diversity is calculated from the same formula, in which p_i now is the proportion of the total foliage lying in the ith designated horizontal layer of foliage.

heights. In order to shift this forest from its present position to one that puts it in line with deciduous and grassland situations it is necessary to double foliage height diversity, or halve bird species diversity (Figure 9), to account for the ability of these birds to partition the outer and inner parts of the spruces. Doubling the number of species present, which accounts for the partitioning between sexes of a species as well as between the various warblers makes the fit to the general regression line even poorer than it now is. This suggests that intersexual partitioning does not seriously modify the species diversity, a conclusion that agrees with the amount of overlap in foraging between sexes and between species, which always is higher between sexes than between species [*25*].

Migration and Wintering Grounds

Up to now I have considered only the contingencies that these birds confront during three to four months of the year. The rest of the year they spend either in migration or on the wintering grounds, which exposes these warblers to conditions strikingly different from the breeding areas. What are the constraints that confront them outside of the breeding season? And how do they relate to the picture seen during the breeding season?

I have portrayed these warblers as denizens of the northern coniferous forests; however, the conditions in these forests are not likely to be duplicated for the warblers during the rest of the year. The individuals that I have studied are located at the southern border of spruce forests in the eastern United States, except for those in the high-altitude forests of the Appalachians. Therefore, upon commencing fall migration most of them quickly encounter new habitats. Not infrequently these new habitats bear little resemblance to a forest, particularly along the Atlantic seaboard where large numbers of warblers migrate. There they may even find themselves on barrier or offshore islands which may have only low tree or shrub vegetation. In some cases no trees may be present. I have observed some of these species on outer treeless islands along the Maine coast. These islands are covered for the most part with grasses, grown rank from the guano of nesting and roosting seabirds, and with varying numbers of emergent flowering herbs, such as angelica and meadow-rue. Being nocturnal migrants, these birds often are reluctant to leave the islands during the daytime, and consequently they must forage there to the best of their ability. Their reluctance to fly during the daytime is generally attributed to the danger of flying predators; indeed, stragglers flying low over the water often are chased by gulls. When on these islands, the warblers prefer the large, broad-leaved forbs, where they are present, over the grasses [*31*]. One might expect that the migrants would experience considerable difficulty in moving through this unaccustomed dense, rank vegetation [*32*]; however, the birds may actually forage in the dense grassy areas.

The species I have discussed, except the Yellow-rumped Warbler, winter almost exclusively within the tropics. The last northern conifers occur in the high mountains of Guatemala; since the majority of most species winter farther south, they do not for the most part have access to coniferous forests at this season. What habitats do they occupy, then? A large proportion of individuals apparently use disturbed or second-growth habitats, or areas at rather high elevations, all being sites in which the resident tropical warblers show the least diversity [*10*]. Unfortunately, information on how they use these areas is sparse, but some observations that I made several years ago in the high mountains of central Costa Rica [*31*] are perhaps illuminating. There, Black-throated Green Warblers wintered regularly in elfin or dwarf oak forests near the timberline about Cerro de la Muerte and foraged in a manner reminiscent of their activities in the northern spruce forests. The leaves of these oaks are long and narrow, almost needle-like. Perhaps this resemblance accounts in part for the conspicuous presence there of Black-throated Green Warblers. They may be exploiting a substrate as similar to the summer one as is possible. Still, it would be naive to suggest that it was a close approximation to spruce foliage from the birds' view. Unfortunately, detailed information is unavailable on the frequency with which wintering warblers forage in habitats that are relatively close matches to their summer ones. MacArthur [*15*] briefly observed several species on their tropical wintering grounds and came to a similar conclusion.

On the other hand, many Yellow-rumped Warblers remain far to the north of the others, a few regularly surviving the winter in coastal New England or even Nova Scotia [*8*]. There, however, they are largely confined to a habitat markedly different from their accustomed breeding areas: coastal bayberry thickets, upon whose waxy berries the warblers largely subsist. In the central and southern United States, Yellow-rumped Warblers become common to abundant during the winter and occupy a wider range of habitats [*24*]. However, even here they are far south of their breeding grounds. In these wintering areas they may feed heavily upon the waxy berries of the wax myrtle, a close relative of the bayberry, or upon the berries of poison ivy. Thus, although many individuals of this species do not migrate great distances, they, too, have forsaken their summer habitats.

Thus, these spruce-woods warblers experience a wide range of challenges throughout the course of a year, which would at first appear to preclude them from developing a high level of adaptation to any one of these situations. Nevertheless, under favorable conditions they pack themselves into an area and manifest a diversity rivaling that of any closely related group of non-migratory songbirds living in the temperate zone. The contingencies that they experience in part result from interactions among themselves, although the importance of this factor varies considerably from species to species and from one population to another. Clearly, the once-common assumption that one population's adaptations realistically describe the species as a whole does not hold here.

Summary

Spruce forests of northeastern North America are unusual in supporting as many as four to six species of *Dendroica* warblers, plus the Northern Parula, *Parula americana*. Each species forages in different parts of the trees, and their foraging maneuvers also differ. Males of a species typically forage higher than their females, a characteristic correlated with the high singing perches of males and the lower sites where nests are located (only females incubate). Females may thus forage in areas not heavily exploited by their mates, presumably advantageous in that females spend most of the incubation period on the nest and have little time for foraging. On small islands containing only part of the normal complement of species, some of the remaining warblers extend their foraging into the parts of the habitat typically exploited by the missing species. These species also have smaller territories than in localities where all warbler species are present. However, the socially dominant species do not change their foraging patterns or

territory sizes on islands containing only part of the normal species complement.

Breeding populations of spruce-woods warblers often are stable, but their numbers sometimes decline markedly. When one such decline occurred, numbers of forest-edge warblers increased (Yellow Warblers, American Redstarts, Northern Yellowthroats). In addition to the species usually present (Black-throated Green, Blackburnian, Yellow-rumped, Magnolia, and Parula warblers), two other species (Cape May and Bay-breasted Warblers) may also occur in the same spruce forests. In many areas they usually are associated with outbreaks of the spruce budworm. When an outbreak is over, their numbers decline and they often completely disappear from the area. During migration and on their wintering grounds, spruce-woods warblers are apt to encounter conditions extremely diferent from those on their breeding areas, which should slow the process of morphological differentiation.

Acknowledgements

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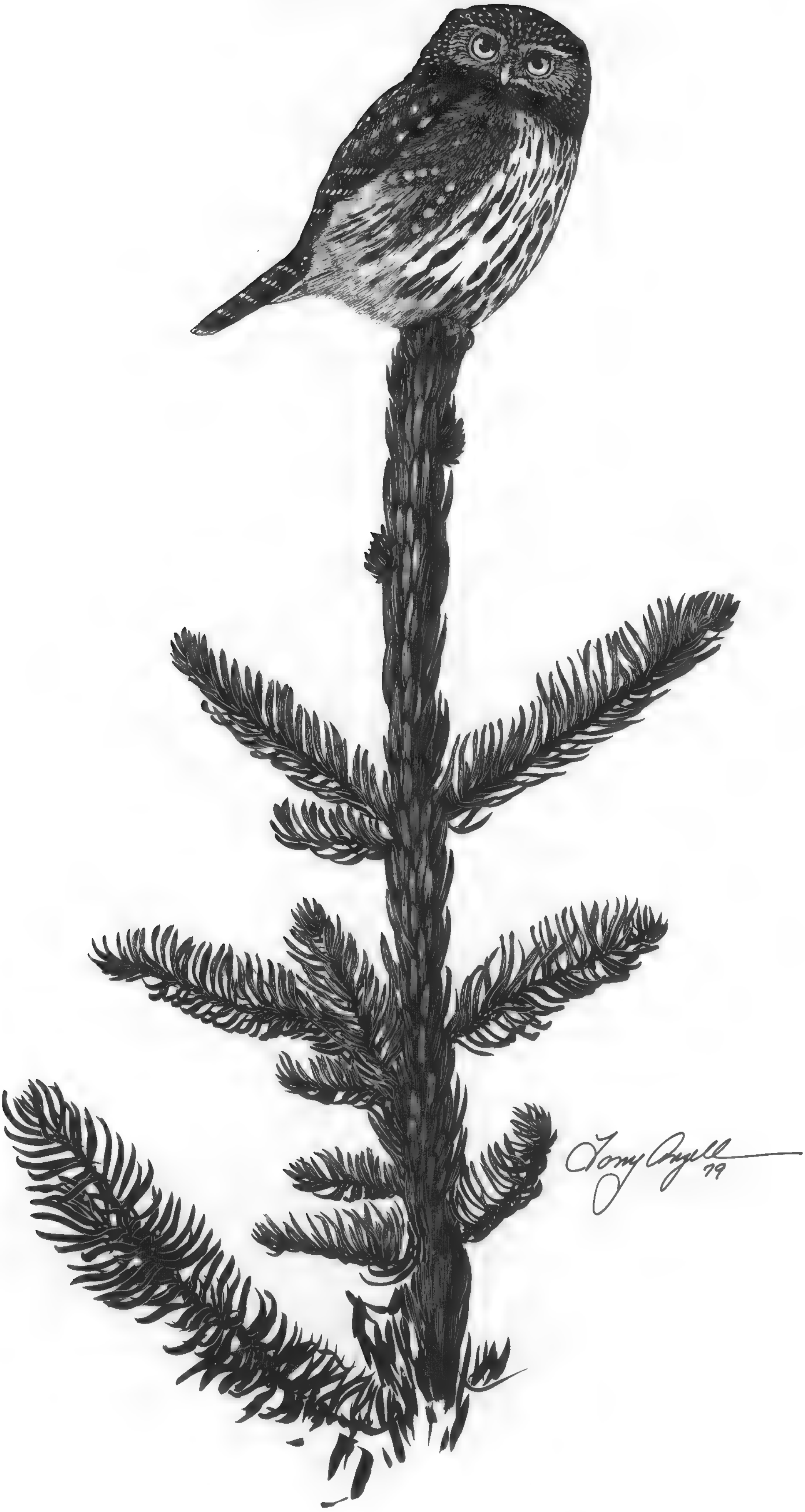
Tony Angell 79

Saw Whet Owl, *Aegolius acadicus*. Drawing by Tony Angell.

BEAUTY AND THE BEAST: NATURAL HISTORY AND ART

ROBERT M. MENGEL

On a cold, windy night in November 1977, I introduced a traveling show of some 30 little-known paintings by Louis Agassiz Fuertes [*1*] at one of our Museum's evening public education programs. I was surprised by a turnout several times larger than expected, as well as by the depth and variety of the questions asked later.

In introducing Louis Fuertes' work, I tried to place him in perspective in the field of bird painting, where after half a century he is still a fresh sensation. More difficult by far, I tried to relate bird art, as it is sometimes called, to Art generally.

The latter generated special interest, which I thought an interesting response from an audience composed mostly of people oriented more to scientific than to artistic endeavors. This stimulated anew my long preoccupation with the enormously complex matters involved in considering Art and the relation of Art to Science. This paper is one result. It is a synthesis of facts and ideas, a few of the latter possibly new, many of them rarely articulated, and often in obscure or widely separted sources. Some are taken for granted by some people while unheard of by others. I do not address the few who are deeply acquainted with the problems of wildlife art and Art (although I would be gratified by any interest on their part). This paper is for those, genuinely curious about wildlife art, who are perplexed in understanding or evaluating it either because of insufficient confidence about Art or inadequate knowledge of nature [*2*]. I beg the patience of those knowledgeable on either side while I attempt to explain things sometimes far from obvious to those on the other.

I have noted recent trends, but individuals mentioned in this essay have been limited to those working up to Louis Fuertes' death in 1927. This may be unfortunate, since more people seem to be painting wildlife today than ever before, and some of them very well indeed. But time lends perspective and historians often consider 50 years the minimum for safety. Also, even were I not guilty of wildlife and landscape painting myself, I would face an impossible test of objectivity in discussing living artists, many of them friends.

While I have often enjoyed criticizing art critics, I find it sobering to be in their shoes. I discover that an art critic needs, aside from some qualifications, strong opinions, iron nerve, thick skin, robust ego, a gift for oversimplification, and the willingness to be wrong more often than might be wished. I embark on the present journey with some trepidation, propelled mainly by strong opinions.

I define wildlife art as drawing and painting (sculpture is equally eligible but not considered) for which wild animals have provided the principal stimulus. I define a wildlife artist as a person who habitually, not incidentally, paints wildlife. I define art as work produced with artistic intent and bad art as a serious degree of failure, given that end. Throughout, when used as nouns standing for their whole fields, Art and Science are capitalized.

Art, Wildlife Art, and Science

Why do we have terms such as "bird art" or "wildlife art" [*3*]? Their frequent use seems to reveal a felt need, suggesting prejudice. Does this mean that wildlife art is regarded, by definition, as a lesser form of art, or bad art, or not art at all, and, if so, by whom? Or does it mean that there is something wrong with animals as subject matter? Subject matter has had a long and tempestuous history in Art, various subjects having been rigorously prescribed and proscribed amid tumultuous debates; but today we are repeatedly assured that the subject is irrelevant to the quality of art. Are wild animals, nonetheless, exempt from this assurance?

George Sarton, a great pioneer historian of Science, has perceptively written that "works of art are precious to us, above all, because they enable us to understand . . . as we could in no other manner, the people who produced them. Each gives us an intuitive, synthetic, and immediate knowledge of their deepest aspirations" [*4*].

Thus, the fundamental attitudes of artists toward animals and nature can be perceived through their works. A recent book *Animals and Men* [*5*], by the prominent art historian Sir Kenneth Clark, is revealing in this respect. The text and, especially, the excellent illustrations are instructive. There are a few examples of Medieval and early Renaissance art, mainly of birds, which show that at least a few artists, such as Antonio Pisanello, were capable of relatively accurate observation of natural objects. Also, with the Renaissance spirit of intense curiosity about everything. Albrecht Dürer studied and drew a few wild animals with dispassionate interest and rare skill. However, almost all of the rest deals with animals of "convenience," that is, of practical importance to man. They are many and often very well painted; animals of utility or pastoral contemplation (cattle, sheep, horses, pigs), of sport (horses, dogs, some slaughtered or dying game), of affection (dogs, horses, cats). There are also animals of fear, such as the ferocious lions of the Romantic period, required to destroy Delacroix's horses and engage his warriors (but which have little to do with lions as lions).

As for wild animals for their own sake, that is, as worthy of understanding and appreciation by the human intellect or spirit, there is virtually nothing. Among the hundreds of artists who have dealt with the subject, only two are mentioned: Thomas Bewick, because of his relationship to wood engraving; and John James Audubon, primarily to show that little progress in accurate (Clark's word) perception of nature had been made in the 400 years since Pisanello.

Although I discuss them later, my object now is not to examine the artistic merit or failings of the painters of wild animals who might have been mentioned, in relation to those of the many painters of tame animals. It is the near obliviousness of Art to a major viewpoint that interests me here. The deep, easily demonstrated, nearly universal ignorance of the natural world that characterizes Art appears to result from the fact that the main stream of occidental Art has chosen to ignore wild animals, along with "wild" nature

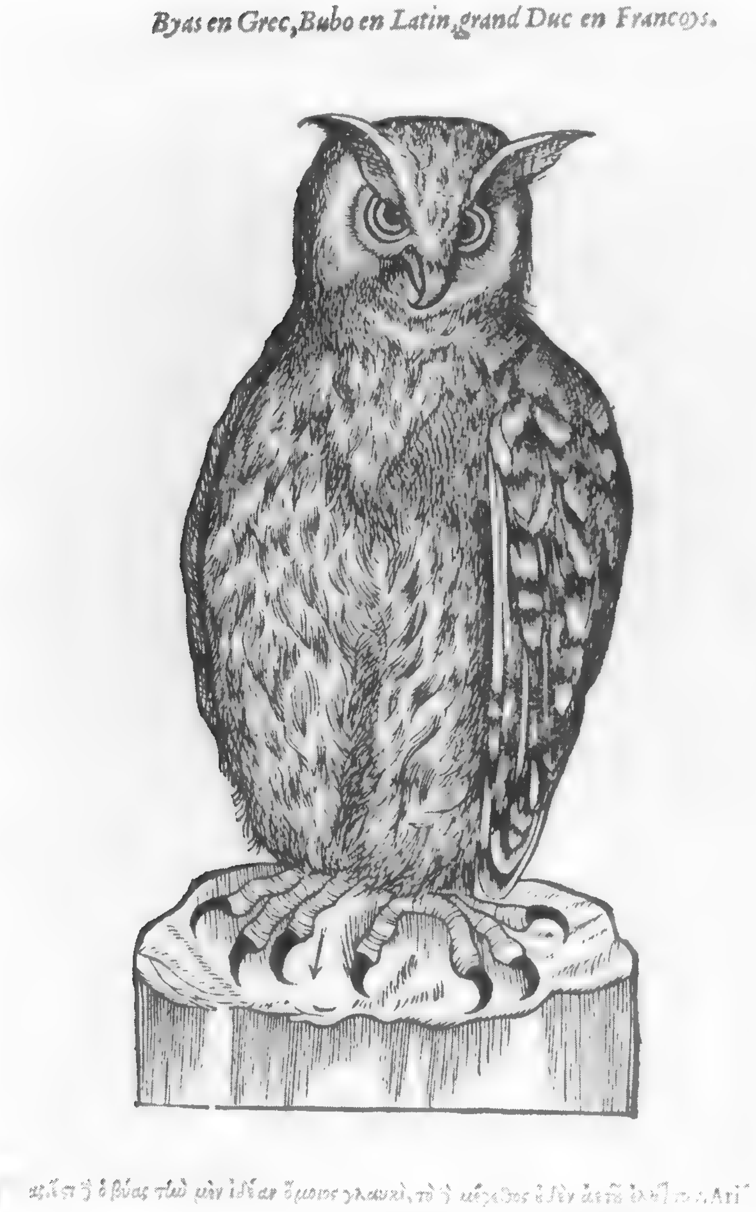
Byas en Grec, Bubo en Latin, grand Duc en Françoys.

Figure 1. A typical woodcut from Pierre Belon's late Renaissance encyclopedic ornithology of 1555 [*27*]. More by inference than by intrinsic evidence, the figure depicts an Eagle Owl, *Bubo bubo*. Note the primitive treatment of the bill, in profile on a full-face view.

generally, dismissing out of hand all who have elected to understand nature. Thus we find Clark stating in his foreword that "no one had ever given much thought to the relationship of animals and men" and able to express surprise (in a book commissioned by the World Wildlife Fund) that men "could *almost* exterminate *a* whole species" (italics mine).

Understanding this condition and how it developed is basic to understanding the position of wildlife art.

Renaissance curiosity led to rapid accumulation of knowledge and proliferation of cultural effort with inevitable specialization. The fundamental dichotomy — indeed, rift — was the one between Science and the "humanities." Science took up the orderly investigation of the universe and the natural world with findings that sometimes dismayed and deeply alienated the humanities (for example, those of Copernicus, Galileo, and Darwin). As the revealing word implies, the humanities, closely reflected by their arts, were almost exclusively concerned with contemplating, and especially with glorifying "God's image" (that is, man) and his works. Deeply ingrained habits of thought die slowly, and the anthropocentric view of the world forged and tempered over several thousand years of Judeo-Christian thought and belief has scarcely been dented by upheavals in Science or religion.

As the humanities (including Art) and Science grew apart following the Renaissance, painters naturally went where the action was — to prestige, power, and money. The sympathetic appreciation and understanding of wild animals that might in a different culture (oriental, for example) have become or remained the province, at least in part, of Art were taken over by Science.

However, although the main stream of Art grew apart from Science, the artistic spirit remained in some of those who pursued Science. Natural history, particularly ornithology and mammalogy, has always attracted many people innately sensitive to the beauty of animals. No other area of Science has had nearly so many devotees who have illustrated their own works or who have hoped that their illustrations would be beautiful as well as functional. The result was the birth of wildlife art, which even in maturity has remained more a province of natural history than of Art. Considering this formidable obstacle, its artistic achievements seem remarkable, however modest they may be relatively.

Some Problems of Wildlife Art

Volume of Effort

Approximately 600 individuals had devoted themselves in some way to bird art up through 1951 [*6*]. By very charitable estimate, 100 of these might be called major bird artists. A crude survey of the most authoritative sources [*7*] yields a comparable but conservative 100,000 occidental painters and other graphic artists considered significant in Art over the same period. Other things being equal, the chances of a good painting being a bird painting are therefore of the order of 1:1,000. But other things are far from equal.

Illustration

Most wildlife artists have been required to be illustrators. This is often a bad word in Art, frequently prefixed by "mere." There is no reason, however, that illustration cannot also be first rate art. Illustration is bad to the extent that it suppresses free artistic conception or restrains free artistic expression. Strong artists survive illustration and even prosper (for example, Hogarth, Winslow Homer, Frederic Remington—I think it was he who quipped that an illustrator is an artist who eats). The weak may be crushed.

While more serious when the sufferer works to please another, the restraints are still there when limits are self-imposed. Audubon depicting all the birds of America was no less an illustrator than Fuertes employed to illustrate the birds of Massachusetts except as he had only himself to satisfy. Neither need the illustration be directed to publication, a point often overlooked. There is the necessity of pleasing the influential client (is it possible that the younger Holbein was unaffected by the penetrating gaze of Henry VIII?) or clientele. Few artists are as free as they think. Bird art, however, has been especially afflicted. For centuries it was virtually a taxonomic "art form" and still has not been fully rid of that albatross.

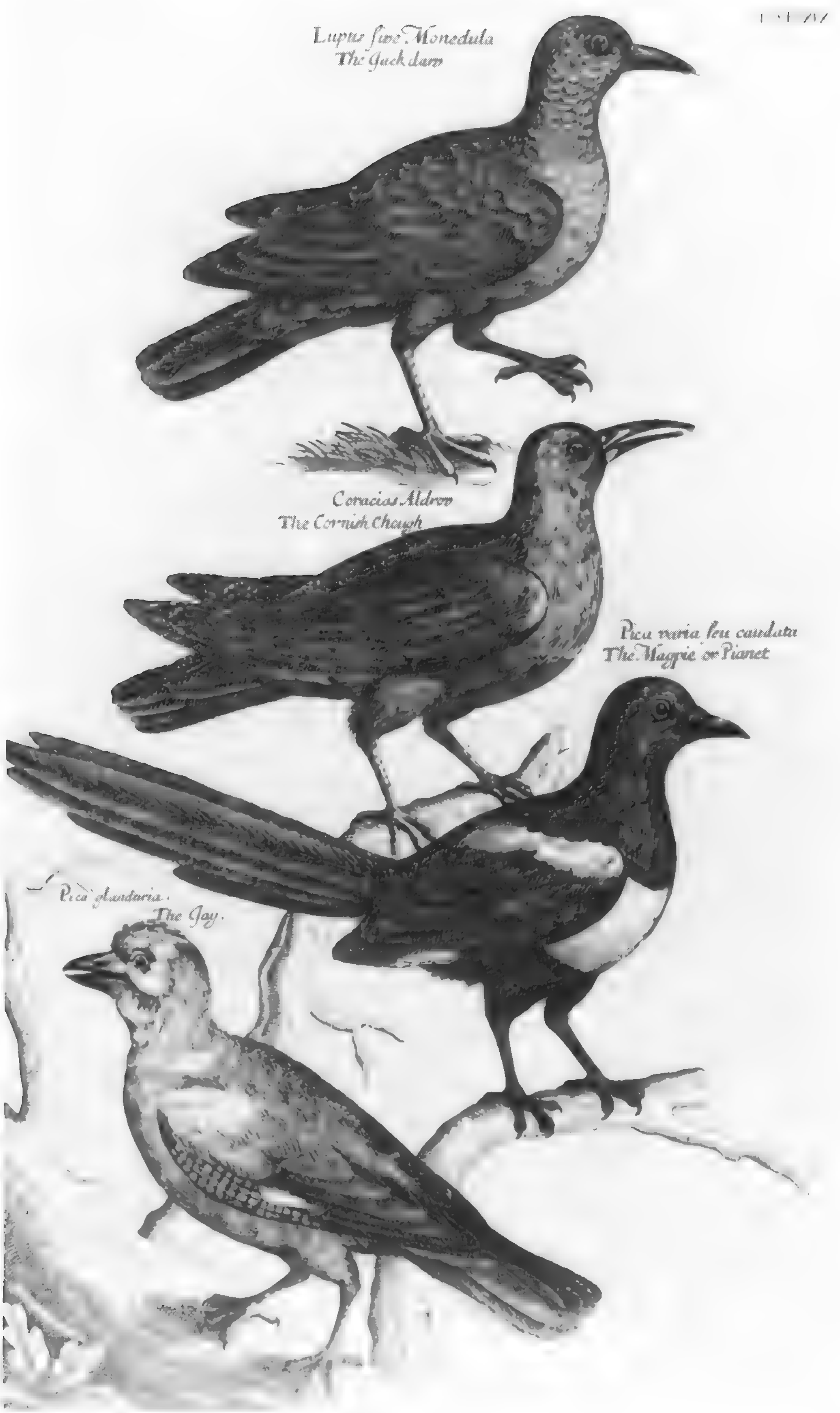
Lupus ſive Monedula
The Jack daw
Coracias Aldrov
The Cornish Chough
Pica varia ſeu caudata
The Magpie or Pianet
Pica glandaria.
The Jay.

Figure 2. Various corvids, depicted in steel engravings from the pioneer ornithology of Francis Willughby and John Ray, 1678 [30] — the seminal work of observational natural history. Technique has advanced markedly since 1555 (cf. Figure 1). Perhaps for the first time in ornithological iconography, the figures reveal critical observation of living birds.

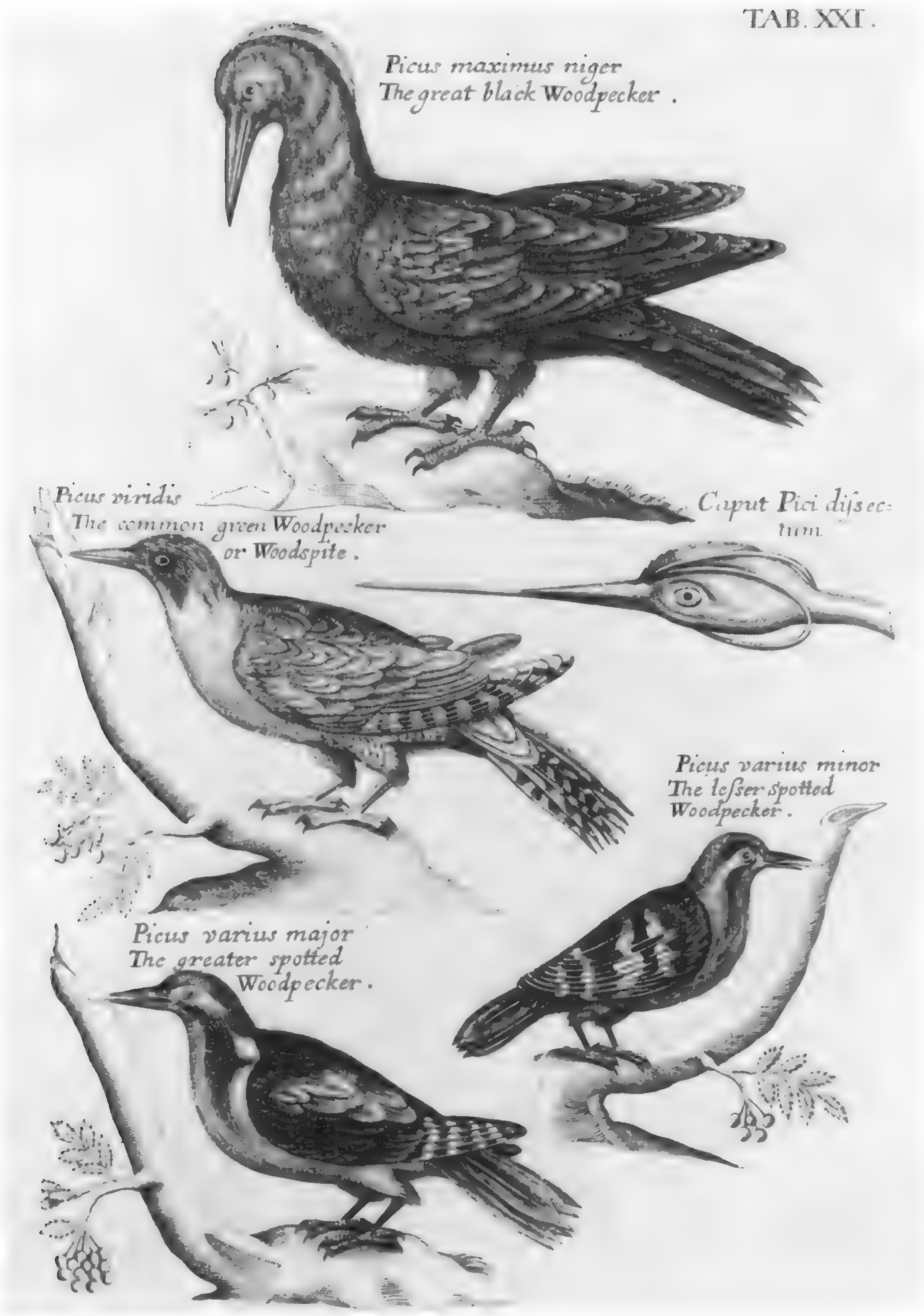
TAB. XXI.
Picus maximus niger
The great black Woodpecker .
Picus viridis
The common green Woodpecker
or Woodspite .
Caput Pici diſsec=
tum.
Picus varius minor
The leſser spotted
Woodpecker .
Picus varius major
The greater spotted
Woodpecker .

Figure 3. Additional birds from Willughby and Ray's ornithology of 1678 [*30*]. Note the early dissection of the remarkable hyoid apparatus of a woodpecker.

Taxonomy and Art

A major business of ornithology for at least 300 years was the discovery and description of new species, which had to be illustrated. The bird artist's first and often only duty, frequently involving little artistic rigor, was pleasing a taxonomic master. The side view thus became conventional, showing the most characters at once. Main concerns were correctness of measurement, selected proportions, numbers of important feathers, local color, and minutiae of bills and feet. Excessive preoccupation with any of these matters is dangerous to artistic expression (one doubts that Rembrandt measured his mother's nose). Very often nobody immediately involved had seen the species alive (laymen have a common misconception on this point, imagining all wildlife artists traipsing through the forest in the image of Audubon).

Then, as later, wildlife artists with rare exceptions received little or no formal training in art and appear mostly to have consulted their fellows for examples rather than the best artists.

Still another problem has been more faunistic than taxonomic. The common requirement of portraying all of the birds of this or that region has resulted in many artists portraying each species once or a few times only. This is no way to gain mastery of any one species or group, which is expected of even the humblest painters of man.

Yet birds are judged beautiful by many people and even stereotyped imitations of their outlines and patterns were often pretty, striking, and colorful as the technical skills of the genre improved. From about 1800 on, they were increasingly provided with "backgrounds," if often seemingly as afterthought. The rapidly accumulating pictures became highly collectible (another danger to art), and so the more enterprising ornithologists sometimes became highly successful businessmen. Their ever more elegant quarto and folio tomes in rich leather bindings graced the library tables of the wealthy, their lists of subscribers the social and royal register of Europe. In his long career, John Gould's illustrators furnished some 45 huge volumes with several thousand different hand-colored lithographic pictures totalling more than a half million individual plates. These still fuel the interior decoration business, rifled from broken sets.

With the Industrial Revolution bird books shrank in size and physical quality but increased in quantity and availability. Their mechanically (soon photographically) reproduced illustrations, however, tended to emulate those of their predecessors, just as early automobiles emulated the carriage, but with some improvement in understanding of the living bird (facilitated, among other things, by improved optical equipment). "Backgrounds" tended to remain secondary and often inept. Collectively, all were the direct ancestors of work, much of it little evolved [*8*], that now satisfies the curious American craze for the "limited edition" print.

The image of a proper bird picture had been fixed in the public mind by essentially ornithological (and often taxonomic) aims, not by primarily artistic ones. This may help account for the fact that some of America's best known recent bird painters, by a sort of convergent evolution, have come to resemble one another almost to the point of confusion. This convergence, interestingly, is less evident in Europe.

Media

An important result of these many years of taxonomic emphasis was that

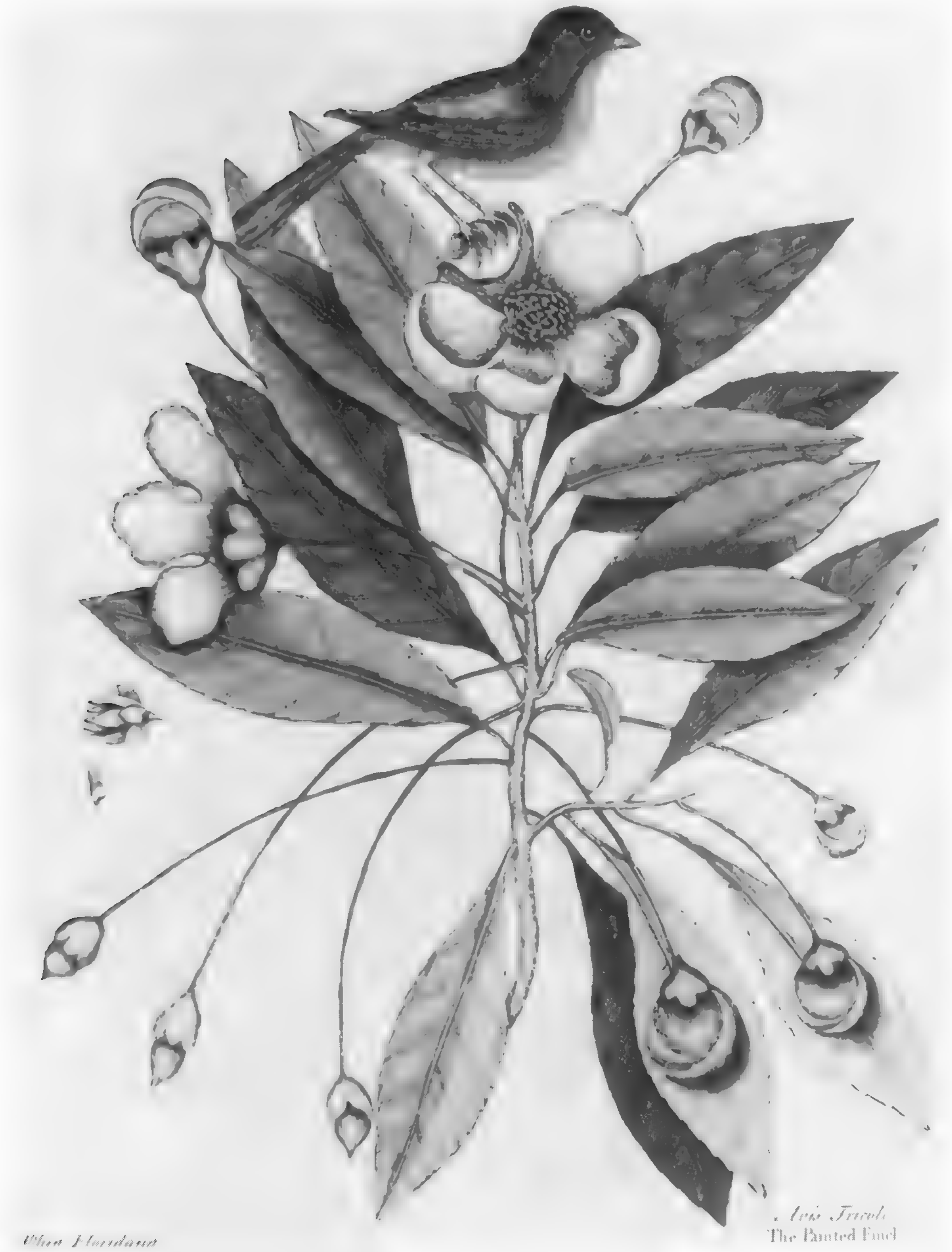

Figure 4. Painted Bunting, from Mark Catesby's *Natural History of Carolina* [etc.], 1731–1743. The floral detail is more loving than any that preceded it (and much that followed) in bird art—indeed it is botanical art.

bird artists, in depending heavily on media that lent themselves to precise rendering of line and to easy correction, were thus almost deprived of two of the more powerful means of expression known to artists, namely oil painting and, at least since Turner, transparent water color. Up until Fuertes' death, wildlife artists working extensively with either of these materials could literally be counted on the fingers.

Until recently, therefore, nearly all wildlife art, when respectable, would correctly be entered in museum catalogues as prints or drawings which are regarded by Art as lesser forms of art.

The Public

It has been said that people get the government they deserve. They also get the art they deserve. Perhaps because much art has grown more esoteric in the twentieth century, we frequently hear the refrain, "I don't know anything about art but I know what I like," as though this confession excuses ignorance about which the speaker has done nothing—not to mention the curious assumption that anyone should be interested in the preferences of a professed ignoramus.

A lot of these people like bird pictures, apparently. The flood of illustrated ornithological books and prints reveals the continued existence of an eager audience, swelled no doubt by the rise of bird watching as a national sport on an economic par with duck hunting and tennis. A large public willing to forgive any shortcoming of a picture as long as it contains a bird virtually ensures the production of much bad art.

I call such work *ornography*. Any picture of a bird "utterly without social or esthetic significance" qualifies. The hard-core ornographer, like George Petty or his more literal descendants of our permissive time, shows top, bottom, front, and most of both sides of an imperfectly conceived bird all in equal light, local color, and exquisite detail.

An excessively detailed picture is not *necessarily* a bad picture but is likely to be. Quality in painting requires substance, the difficult capture of essence and structure which detail obscures. One must ask why the successful would wish to conceal their skill. Alexander Pope [*9*] cannot be improved upon:

> Poets, like painters, thus unskilled to trace
> The naked nature, and the living grace,
> With gold and jewels cover ev'ry part,
> And hide with ornaments their want of art.

Nevertheless, detail is a popular passion with American bird painters, suggesting a great demand or need for it.

Regularly I learn of yet another bird artist said—another danger signal—to be the "greatest since Audubon." Surely there are 100 by now.

The uninitiated might reasonably ask how all 100 can be greatest at once. It is easy when the stated criterion is detail. Take feather barbs, visible in nature at not more than four feet in good light—two feet if you are over 40. The average bird may have 2,000,000, give or take a few. Multiply by several birds, throw in mineral and vegetable minutiae, and the number of details approaches infinity. Nobody cares enough which painter is "greatest" to settle the matter by actual count.

Why Some Good Wildlife Painting Goes Unappreciated by Art

Given all that has just been said, it is really remarkable that so much wildlife art has been good.

No matter what is said about the irrelevance of subject matter, there is evidence that considerable prejudice against wild animals exists in Art, varying with time and place. Carl Rungius encountered it, as noted beyond, and there are examples back to Joseph Wolf. I began by noting the disinterest of anthropocentric western man, and Art, in wild animals, but disinterest seems inadequate to account for the evidence. Outright aversion is more to the point [*10*].

"Ugh, a frog!" "Kill it, it's a snake." "Damned environmentalists!" It seems optimistic to suppose the Art world is free of these attitudes which pervade our society. Ignorance begets fear; fear begets hostility; hostility leads to ridicule.

Another kind of prejudice also has roots in ignorance. The basic cause of

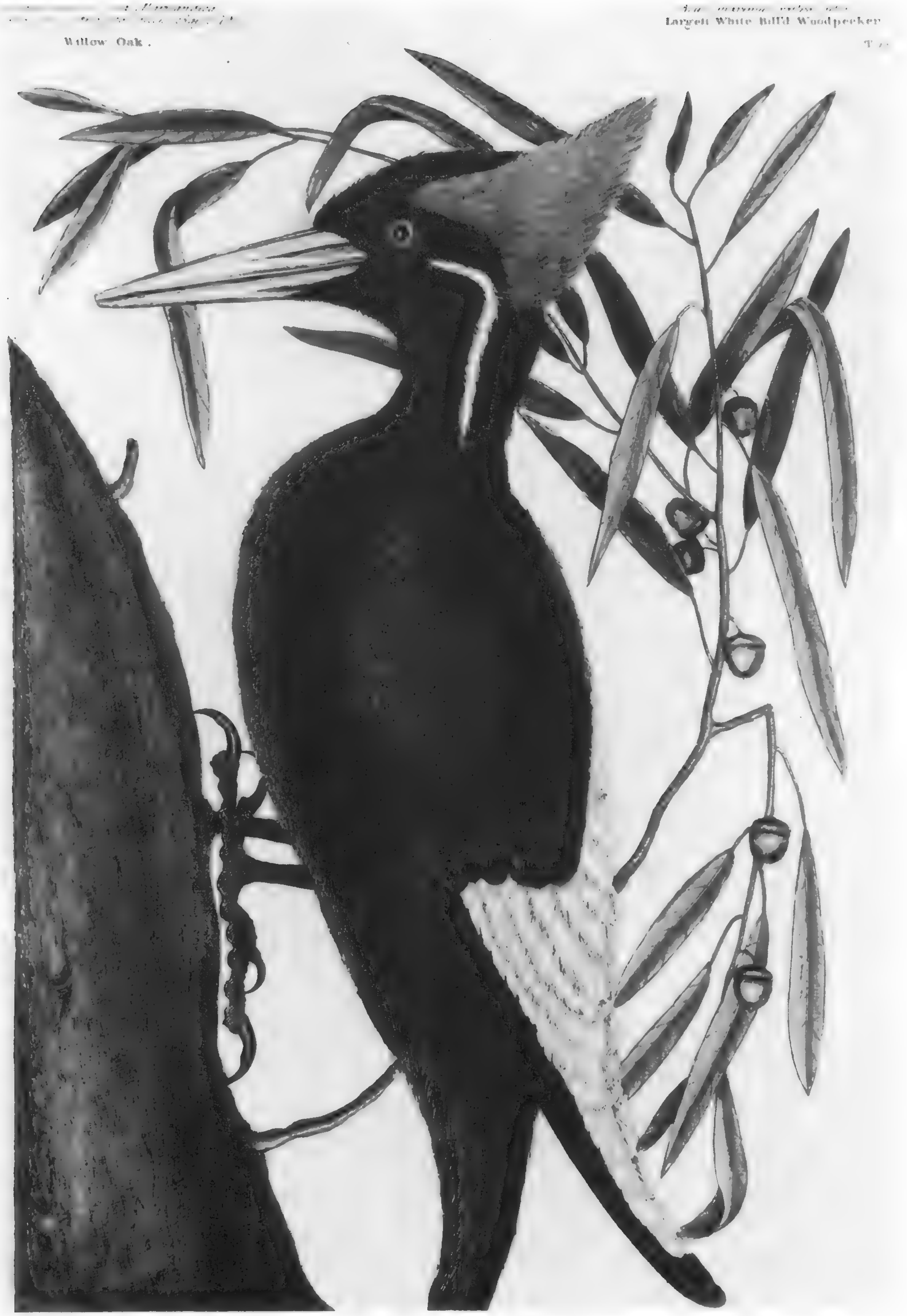
Willow Oak.
Largeſt White Bill'd Woodpecker

Figure 5. The "Largest White Bill'd Woodpecker" (= male Ivory-billed Woodpecker, *Campephilus principalis*), the 16th plate in Catesby's *Natural History of Carolina* [etc.]. Catesby's birds were the most spirited and his work the most ambitious of its kind, to its date.

it is bad taxonomic art from which, by extension, careless thinkers conclude that *any* truthful perception of a wild species precludes art. The loaded words are *accuracy, correctness, photographic*, and *mere*. Almost never is the critic or juror able to judge these matters with respect to wild animals, while forgetting that, if penetrating truth to a species precludes art, then exit Rembrandt, Leonardo, Holbein, Reynolds, and so on.

There are, in other words, different kinds of accuracy, which Art already knows perfectly well. The difficulties are most clearly revealed by the fact that it seems necessary to say this. Biologists, especially taxonomists, are prone to be hung up on taxonomic accuracy, the only kind many of them *can* evaluate; Art authority is unable to judge any kind of accuracy here, blinded both by ignorance and misconception.

There is the accuracy of the engineer's drawings of an automobile [*11*]. No one ever sees an automobile that looks exactly like that. The drawing, which may be beautiful in its own right as related to function, proportion, and rendering, is *taxonomically accurate*. Automobiles in nature, however, are affected by light, shade, distance, motion, perspective, and wear, which variously distort, obscure, or accentuate the taxonomic characters. Essence remains. Accurate perception of automobiles in nature requires, for a painter, putting down what is seen, or seems to be seen, in a particular context or moment. Insistence upon showing what may not be seen is deleterious to accuracy in this sense [*12*]. A moment or event in nature also evokes intellectual and emotional responses in the viewer (artist). The automobile may be bearing down upon one at high speed out of a blinding rainstorm. These responses are based on *particular* features of what is seen,

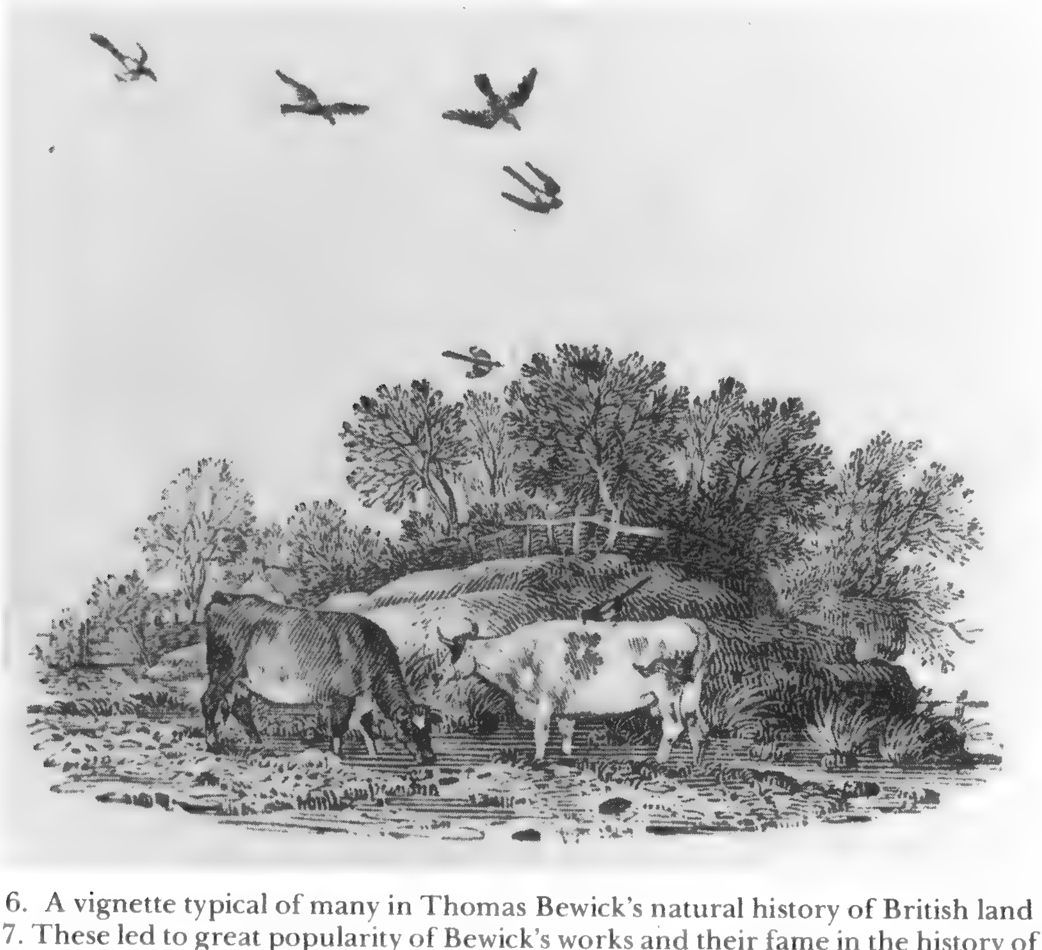

Figure 6. A vignette typical of many in Thomas Bewick's natural history of British land birds, ca. 1797. These led to great popularity of Bewick's works and their fame in the history of wood engraving as well as for their perceptive, sometimes salty, glimpses of English rural life and manners.

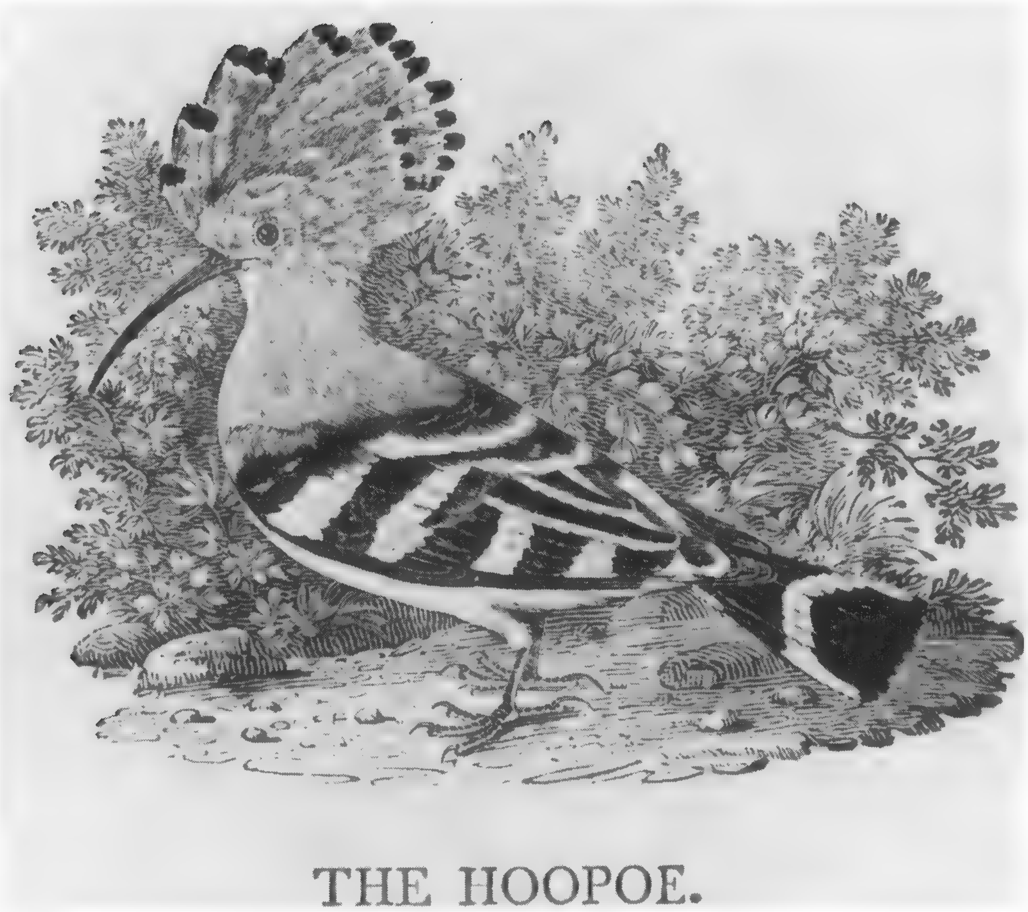

Figure 7. The Hoopoe, *Upupa epops*, from Bewick's "land birds" of 1797 (see also Figure 6). Although usually stiff and shown side view, Bewick's birds reveal penetrating observation of birds in life, unprecedented among ornithological artists.

or implied by it (the headlights and gleaming bumper may look particularly significant). They will differ with every artist and every viewer. Intelligent selection and emphasis of these features, to some end, is the main business of art. That involves the isolation of meaning. Through all of these stages, various taxonomic characters may persist (the automobile that is about to destroy us may be clearly a Chevrolet) and, in the absence of artistic reasons to the contrary, taxonomic characters *should* persist.

The perception of essences is critical, in wildlife art and elsewhere. By essence I mean special character, unrelated to dress, detail, features. We know our good friends in the rain, muffled in coats, at half a city block. From the highest row of seats, the devoted football fan knows which back has the ball, without benefit of number. In poor light and a moment, a gifted field ornithologist recognizes obscure species that challenge beginners under ideal conditions.

The gifted animal painter comprehends these distinctions, his quickly sketched outlines requiring no feathers or details for recognition by fellow intellects. They may be exaggerated in significant features, for various reasons, just as El Greco, Goya, John Steuart Curry variously exaggerate human characters. Louis Fuertes' falcons are quintessential falcons, radiating the special qualities of their kinds with extraordinary fidelity of spirit. Each of Carl Rungius' many moose is not only an individual from many in the artist's vast experience, but also prototypical.

The recognition of essence may require refined understanding which even many otherwise capable naturalists lack. I have known respectable

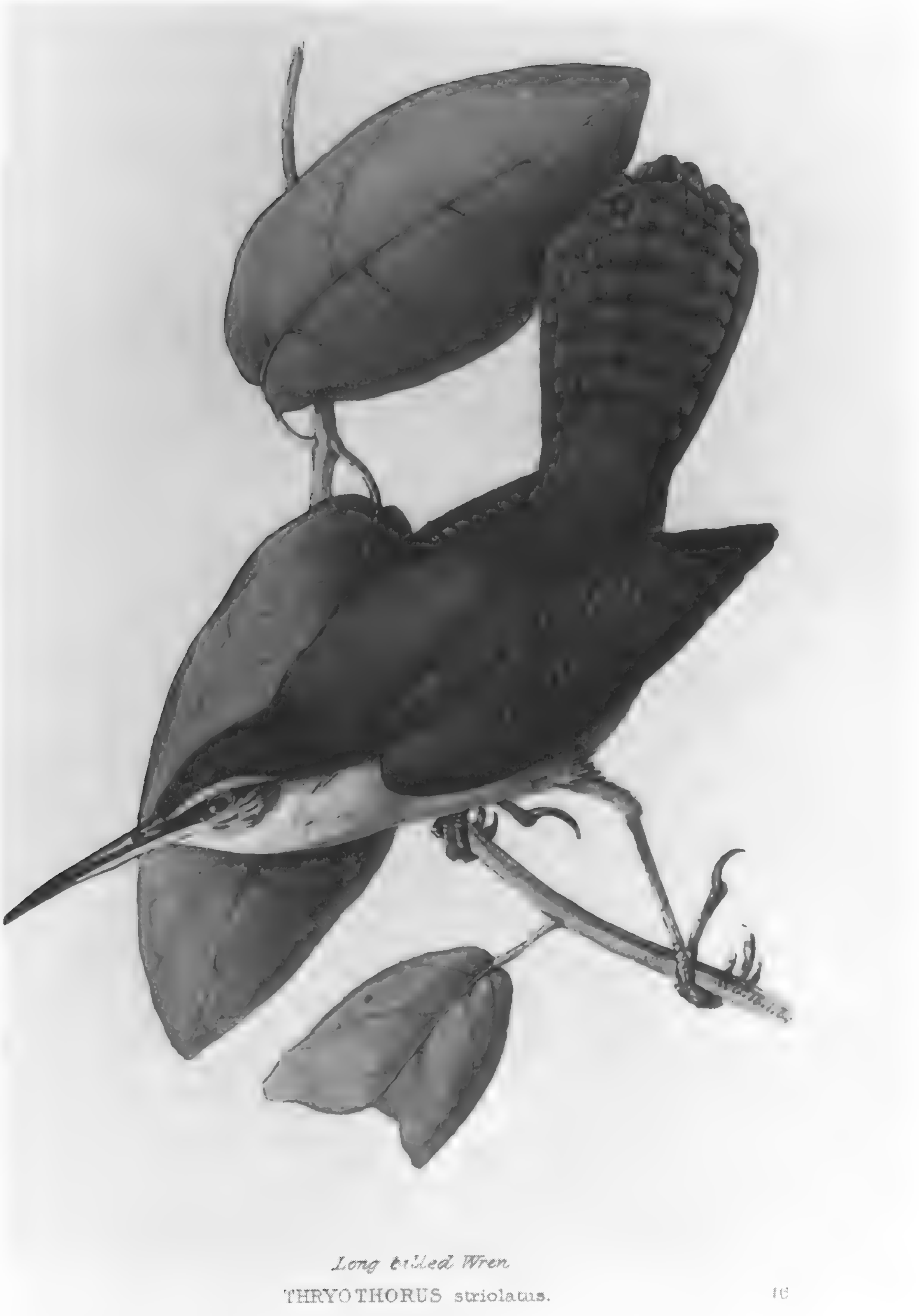
Long billed Wren
THRYOTHORUS striolatus.
16

Figure 8. A tropical relative of our Carolina Wren, from William Swainson's *A Selection of the Birds of Brazil and Mexico*, 1841 (the drawings date from 1834–1836). Doubtless influenced by his friend Audubon, Swainson was nevertheless among the first to show decidedly animated birds in his unassuming but very well drawn pictures of high ornithological accuracy.

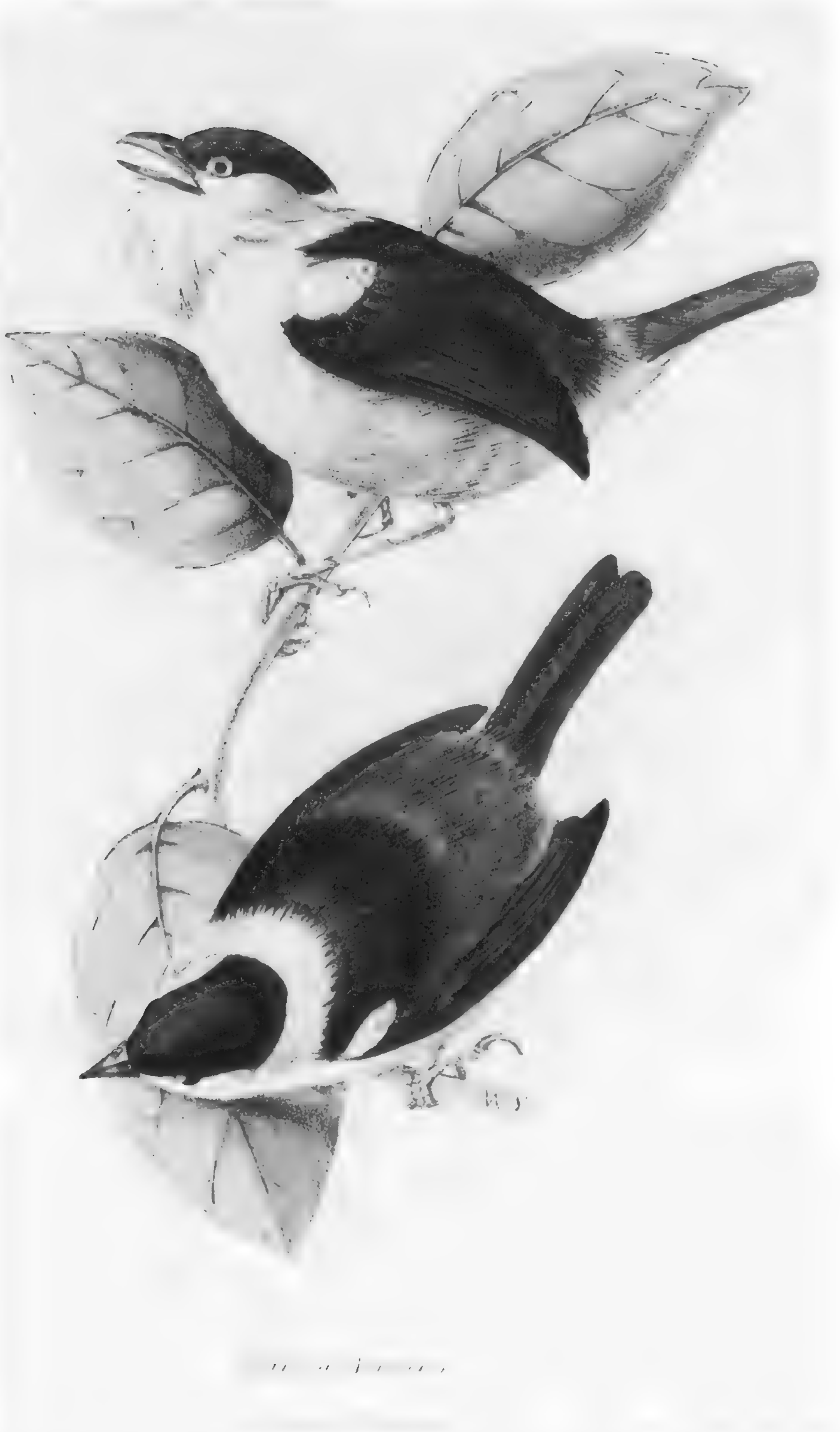

Figure 9. A manakin from Swainson's drawings of Brazilian and Mexican birds (see Figure 8). This is a very precocious drawing for its time.

ornithologists unable to see qualitative differences between Louis Fuertes' birds and those of Allan Brooks, which is equivalent to confusing Tchaikovsky with Rudolf Friml.

In stressing essence, however, I am not stressing identification in the taxonomic sense at all, nor even sympathetic description. To capture essence means to make known the character of a thing, and its meaning in relation to other things, importantly including its meaning to the artist who wishes to share it. This is true in all art and is esoteric in wildlife art only because most humans, broadly familiar with their own species and its commensals, have almost no acquaintance with other species.

It seems optimistic to expect much of this kind of perception from conventional Art authority, even in the rather unlikely event of sincere effort.

There are, however, welcome signs of increasing tolerance if not perception. Shows devoted to bird painting have recently been held at several conventional art galleries or museums (e.g., Chadd's Ford, Pennsylvania, 1973; Sandwich, Massachusetts, 1978; and Wausau, Wisconsin, annually since 1976). Here and there, paintings of, or including, wild animals are gaining admission to regular juried shows. If this indicates a new trend, future historians may look to its causes. Perhaps the flickering flame so long nursed by natural history will be passed on to an Art of enlarged awareness.

Landscape and Nature

Until now we have considered the portrayal of wild animals as such. In the real world, however, things do not exist apart from their surroundings. This leads to the subject of landscape, wherein it might be supposed that Art and wildlife art would find common ground. That there is comparatively little should not, by now, be very surprising.

Landscape, Clark [*13*] correctly said, "marks the stages in our conception of nature." He recognized several ways of looking at nature, of which the "landscape of fact," whose first purpose is descriptive, is of principal interest here.

"Facts become art," Clark truly says [*14*] (if in the lofty idiom of his genre) "through love, which unifies them and lifts them to a higher plane of reality. . . ." Great skill is also required for this love to succeed; but for numerous reasons, as we have seen, few wildlife artists have treated landscape with competence, let alone distinction.

The very rare contribution of the very few who have painted significant landscape will not be fully appreciated without another look at history. This brings us to the admonitions of Genesis, wherein untamed nature is seen as a threat to be subdued as rapidly as possible, and again to the generally anthropocentric view of the world that is a consequence.

> So God created man in his own image . . . and God said to [him], "Be fruitful and multiply, and fill the earth and subdue it; and have dominion over the fish of the sea and over the birds of the air and over every living thing that moves upon the earth."
>
> Genesis, 1:27, 28

In the great tradition of European Art, landscape was long painted mainly as theatrical backdrop for the glory of man and his works, emerging as a major art form in its own right only in the nineteenth century. Even then the great naturalistic painters (e.g., Constable, Turner, Corot, Courbet)

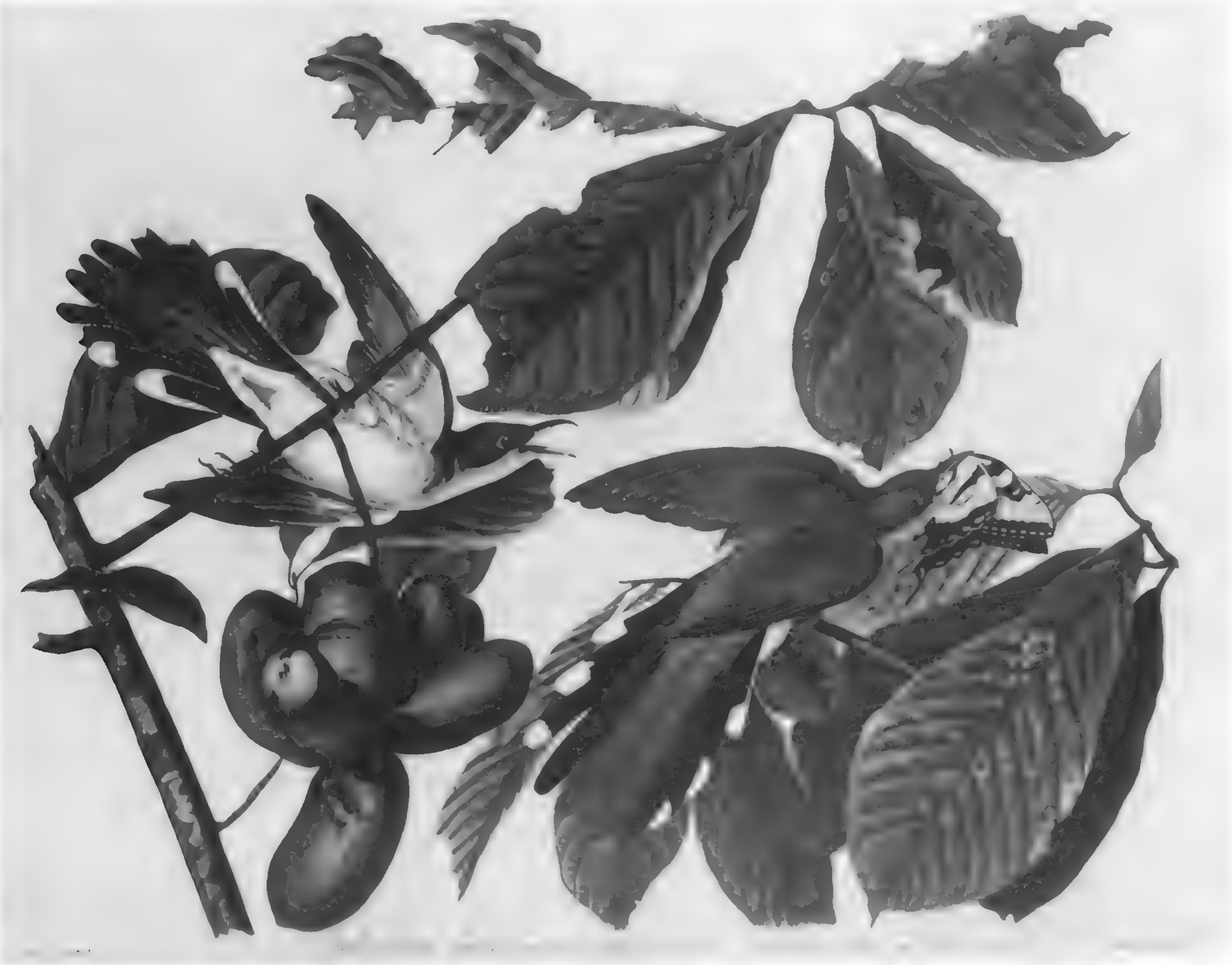

Figure 10. John James Audubon's pictures remain among the best composed prints of all time, in "bird art" or elsewhere, as shown in his treatment of the Yellow-billed Cuckoo, Plate 2 of *The Birds of America*, 1827.

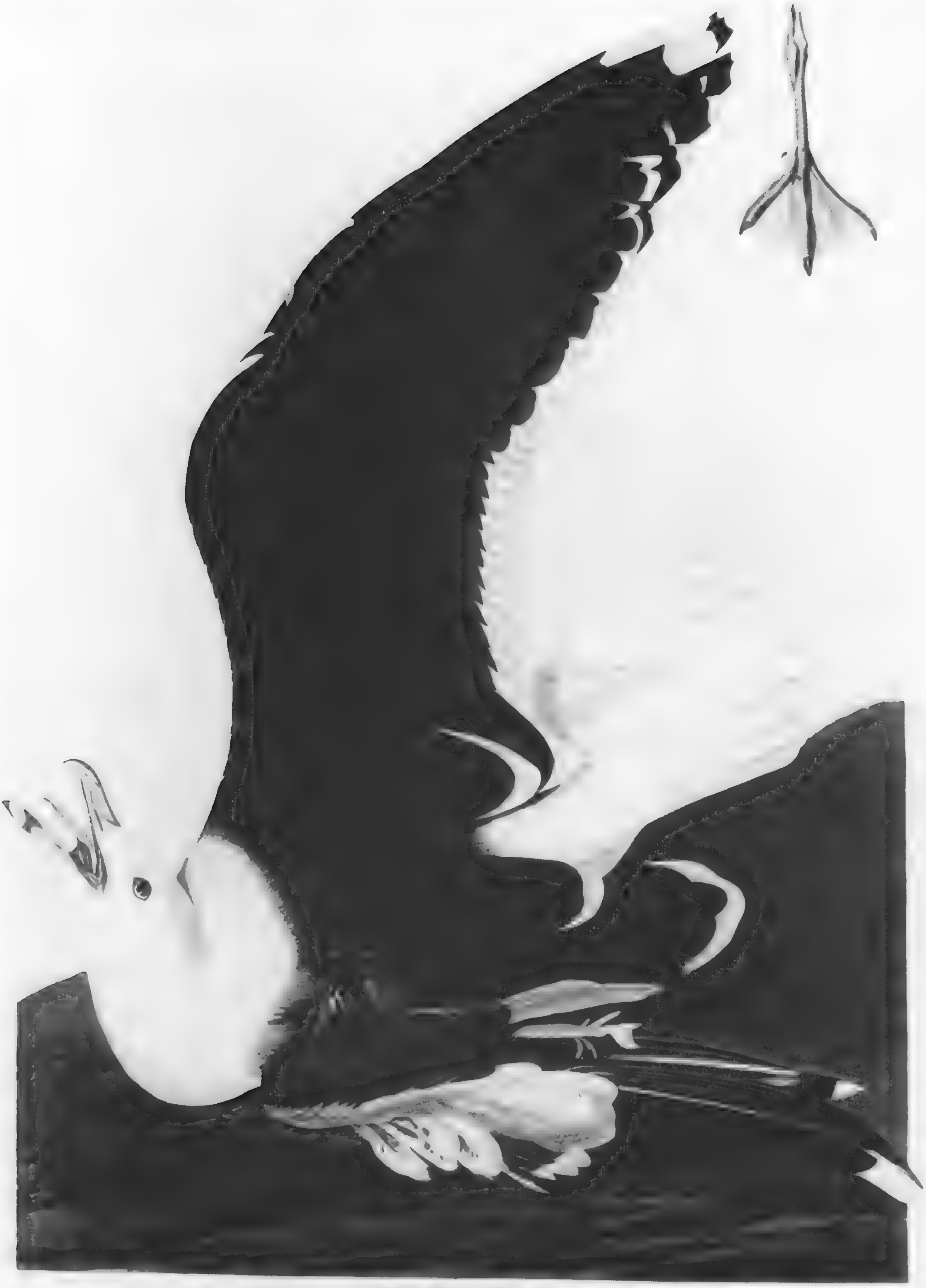

Figure 11. Audubon's martyred Great Black-backed Gull (Plate 241, *The Birds of America*, 1835) is one of many of his pictures which suggest human emotions (see text and note 36). For notes on dating see W. Stone, *Auk*, 23:298–303, 1906.

considered it justified mainly because, as Constable thought, "nature was the clearest revelation of God's will" [*15*]. However well painted, their "nature" was the cultivated countryside of Europe, which had rarely threatened anyone for centuries. Wilderness, other than as fantasy, was scarcely painted at all. Exceptions are found in some seascapes and in the brief attentions of J. R. Cozens and J. M. W. Turner to the Swiss Alps.

Wilderness entered landscape with significant frequency only with the opening of America. The assorted romantic "poets" of the "Hudson River School," attempting to compensate for deficiencies in comparison with the art of Europe, thought to lessen the latter by glorifying the "unsullied" American landscape of the "wild" Hudson valley. But they still saw with European eyes. With Asher B. Durand [*16*], they believed that "landscape will be great ... as it declares the glory of God, be a representation of his works, and not of the works of man." Works of man or no, the anthropocentrism is thinly veiled; untamed or otherwise, nature is still seen as *for* man.

As wilderness, the early Yosemite paintings in the Hudson River spirit by Albert Bierstadt are as "wild" as a Victorian drawing room [*17*]. His misty utopia suggests a florid dream of Manifest Destiny.

But with the tide of western expansion an unprecedented number of intrepid artists [*18*] painted wild nature in one way or another, to the great benefit of history, and some with clear and objective eyes unusual in nineteenth century art. Early, the A. J. Millers, George Catlins, and Carl Bodmers reported the factual landscape of the bison-dotted plains and shining mountains with varied skills and visions. Thomas Moran painted the Yellowstone country with romantic flourish but with observation infinitely sharper than Bierstadt's. Some romanticized the "Noble Savage" while other romantics of different persuasion saw a wild menace [*19*] to be conquered with all speed (and lots of excitement, too). Last were the "cowboy and cavalry" artists — the Remingtons, Schreyvogels, and C. M. Russells, who viewed the sharp western landscape with the cool, knowing detachment of a frontier scout. They painted a wilderness "landscape of fact," however raised to art, that is recognizable to naturalists.

Whether or not some of them approached it, consciously or otherwise, there is a way of regarding nature other than the anthropocentric one; and how nature is regarded must affect the way in which nature is seen. At least in the West, this way seems to be almost the sole property of naturalists and is consequently still quite rare. This way abandons *without fear or resentment* the classical tenet that nature was created solely for the benefit of man. Nature is neither enemy nor servant, hence neither benign nor hostile. Nature rewards adaptation and punishes the unadapted. The lion does not lie down with the lamb in anthropomorphic bathos, but they are exquisitely interdependant. Nature is an impartial, intricate, and elegant system within which man stands and falls equally with all other life, unique only in the quality of awareness and the responsibility of intelligence. Of this magnificent universe it is quite as possible to be reverent, if art requires reverence, as it is to be reverent of the various intellectual constructs created for man's reassurance and glorifi-

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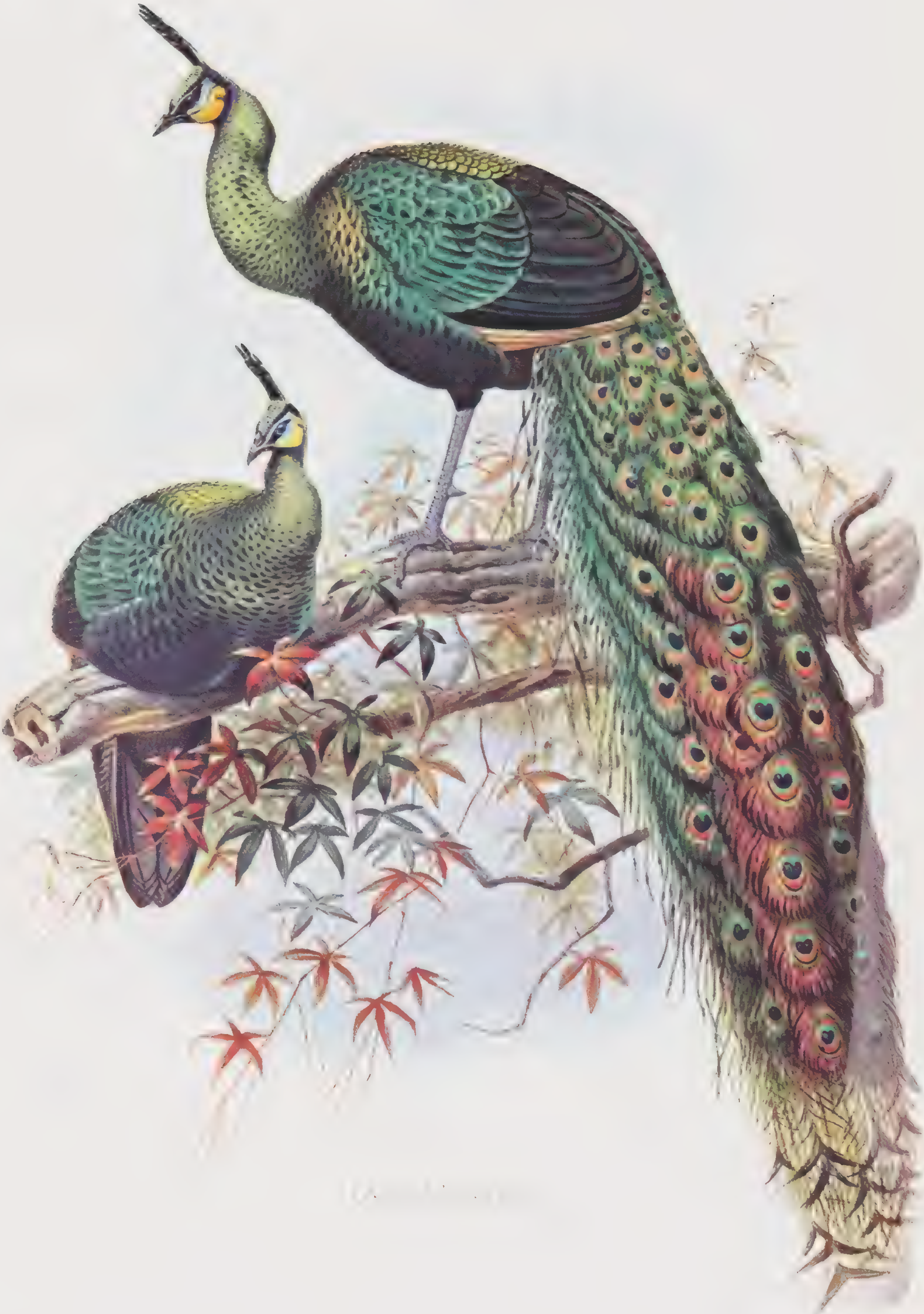
Plate 1. Of the great 19th century ornithological monographs, none save Audubon's is so sumptuous as D. G. Elliot's *Monograph of the Phasianidae, or Family of the Pheasants*, 1870–72, a rare American contribution to this elegant class of books. It was entirely illustrated by the incomparable Joseph Wolf, one of its loveliest plates being the present one, showing the Green Peafowl, *Pavo muticus*.



cation. In literature this viewpoint may find its clearest spokesman in Henry David Thoreau, a century ahead of his time.

If the hothouse spirit of the narcissist withers before these ego-deflating perspectives [*20*], other spirits are exhilarated. They accept equal membership in the stream of life and relate to it with respect, understanding, and love. For them this exhilaration, *a necessary condition for the full life*, is most readily and most purely experienced in wilderness [*21*].

Wilderness, wild nature, fully reveals her many meaningful and subtle essences only to those who know her well and accept her on her own terms. It is not surprising that gifted painters of wilderness with the necessary hardihood, knowledge, and sympathy, with vision unhampered by moralistic cant, romantic sentiment, and apocalyptic claptrap, have been very rare indeed. Winslow Homer was one of the first major painters, probably the greatest, and remains one of the very few, to seek out and paint wilderness landscape with these qualifications [*22*]. They were also the property of Carl Rungius and Bruno Liljefors. There are others, and will be more.

Some Representative Artists

There is space only to discuss a few artists who have given new direction to bird or wildlife art, exemplify various kinds of work, or who have been especially successful. I cannot even discuss all of the last; the work of some, for example Richard Friese, Johannes Larsen, and Leo Paul Robert, has simply not been adequately accessible to me.

Given more space I should certainly have discussed more people outside the conventional boundaries of natural history, such as gifted magazine illustrators like Charles Livingston Bull and fine mammal painters like Paul Bransom. Also I would have given space to etchers such as Frank W. Benson and gifted wildfowl painters like Richard E. Bishop, whose audience has been primarily hunters. Indeed, it should be recognized that the shooting fraternity, in the last century or so especially, has conspicuously shared natural history's burden of keeping wildlife art alive and growing.

The true hunter and the true naturalist have much in common and share a genuine love of animals that perpetually mystifies humanists like Kenneth Clark, who sometimes grant but rarely understand it. It must be very ancient and may be more readily understood in relation to predation and another widespread misunderstanding. As Konrad Lorenz showed us in *Man Meets Dog* [*23*], "ferocity" in animals is related largely to fear. Predators approach their normal prey with the same benign interest and appreciation that we approach a savory roast or pie. Hence all the snarling lions and wolves attacking deer and hapless maidens in art and literature are figments of the human imagination. Besides atavistic predatory (that is, food-getting) urges, modern hunters and naturalists add esthetic appreciation and intellectual curiosity, both of which may be extremely intense. It is no accident that such great wildlife artists as Audubon, Fuertes, Rungius, and Liljefors have been vigorous hunters.

I have necessarily concentrated on artists significantly and regularly interested in wildlife. A considerable number of Americans, some of them important, who have occasionally treated wildlife subjects, are interestingly treated and well figured in Haverstock's *An American Bestiary* [*24*]. Many other conventional wildlife artists, fortunately, are discussed at length by both Anker [*25*] and Nissen [*26*].

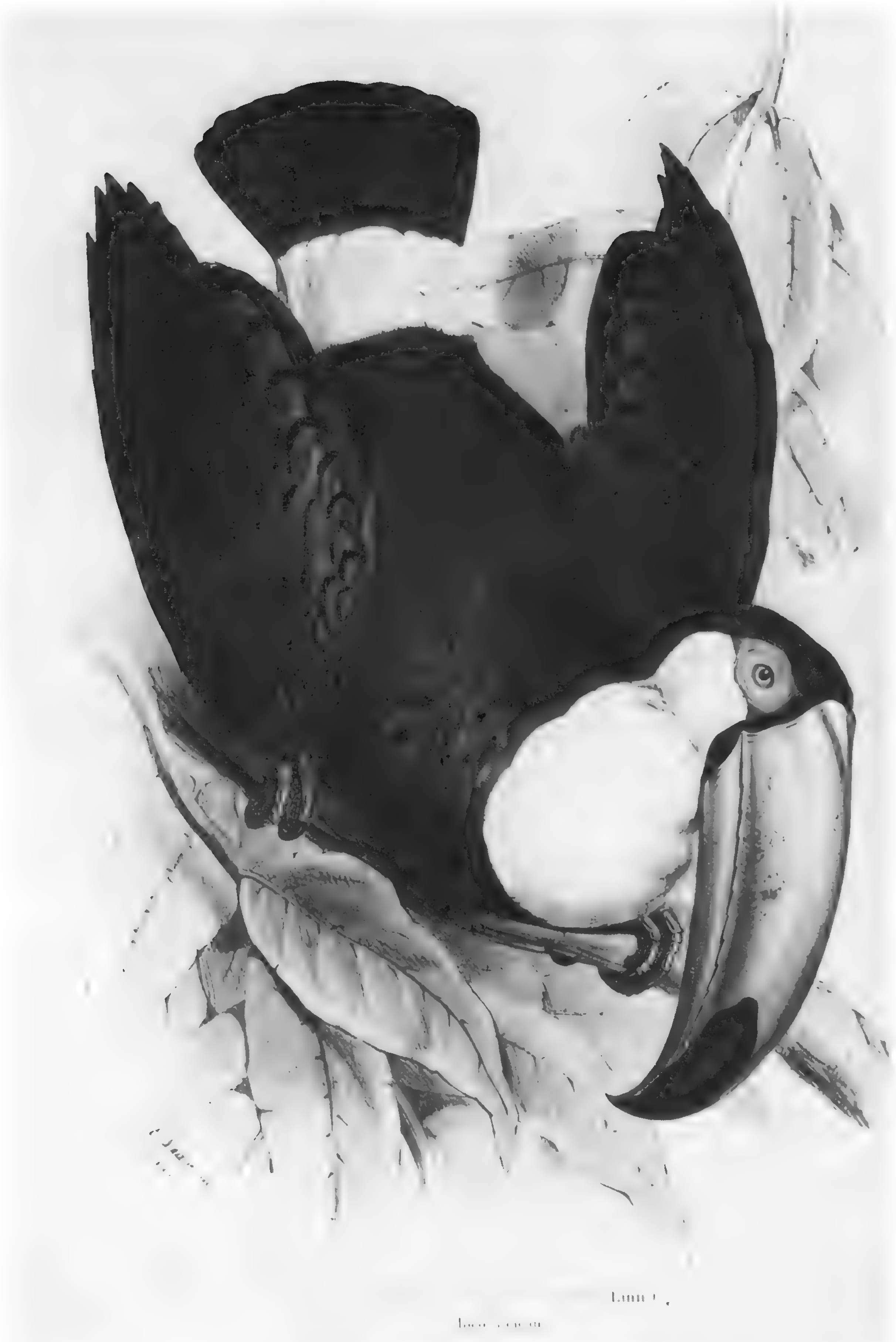


Figure 12. Edward Lear (1812–1888), noted British writer and draftsman, was a decided cut above most of the several illustrators (see text) who collaborated in the multitudinous productions of John Gould. His few contributions, like this toucan, *Ramphastos toco*, from *A Monograph of the Ramphastidae, or Family of Toucans*, second edition, 1852–1854, are unusual among Gould plates in being signed by the artist, who, further, is credited on the plate *both* as delineator and lithographer.

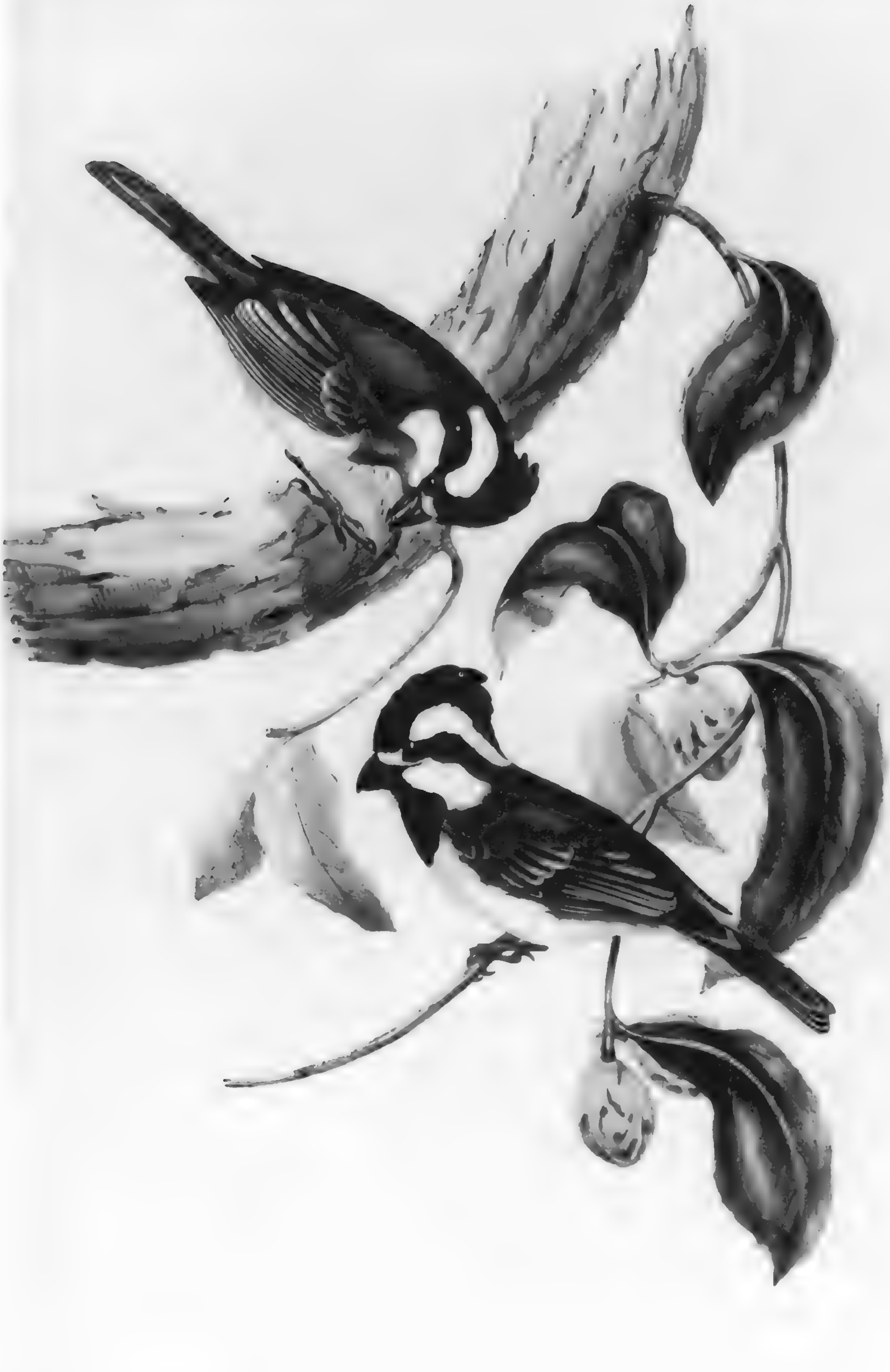


Figure 13. Elizabeth Gould's hand is responsible for this plate of the Eastern Shriketit, *Falcunculus frontatus*, from *The Birds of Australia*, 1840–1848. Although the hands and styles varied, this is typical in spirit and quality of the great majority of Gould's several thousand illustrations (see text).

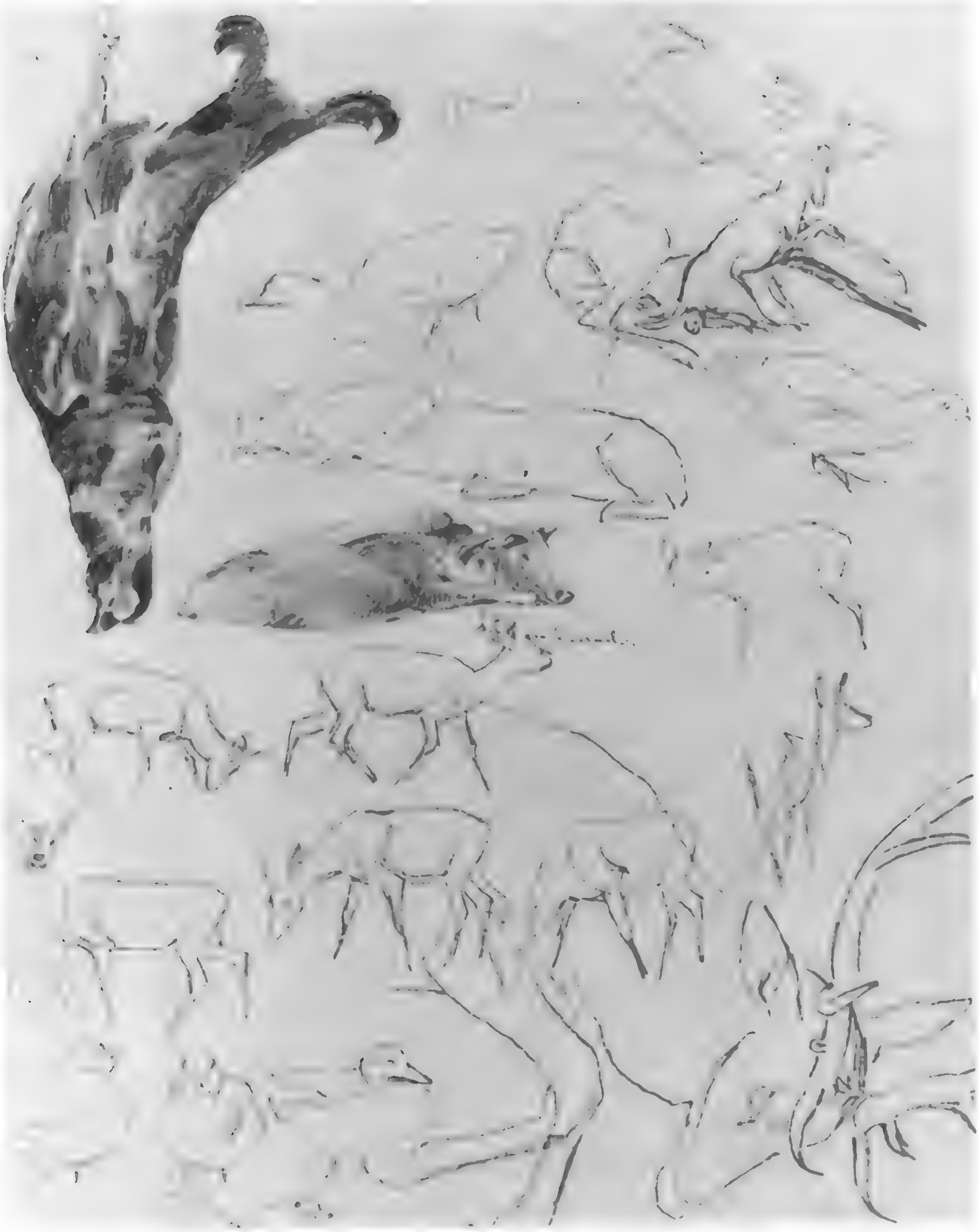
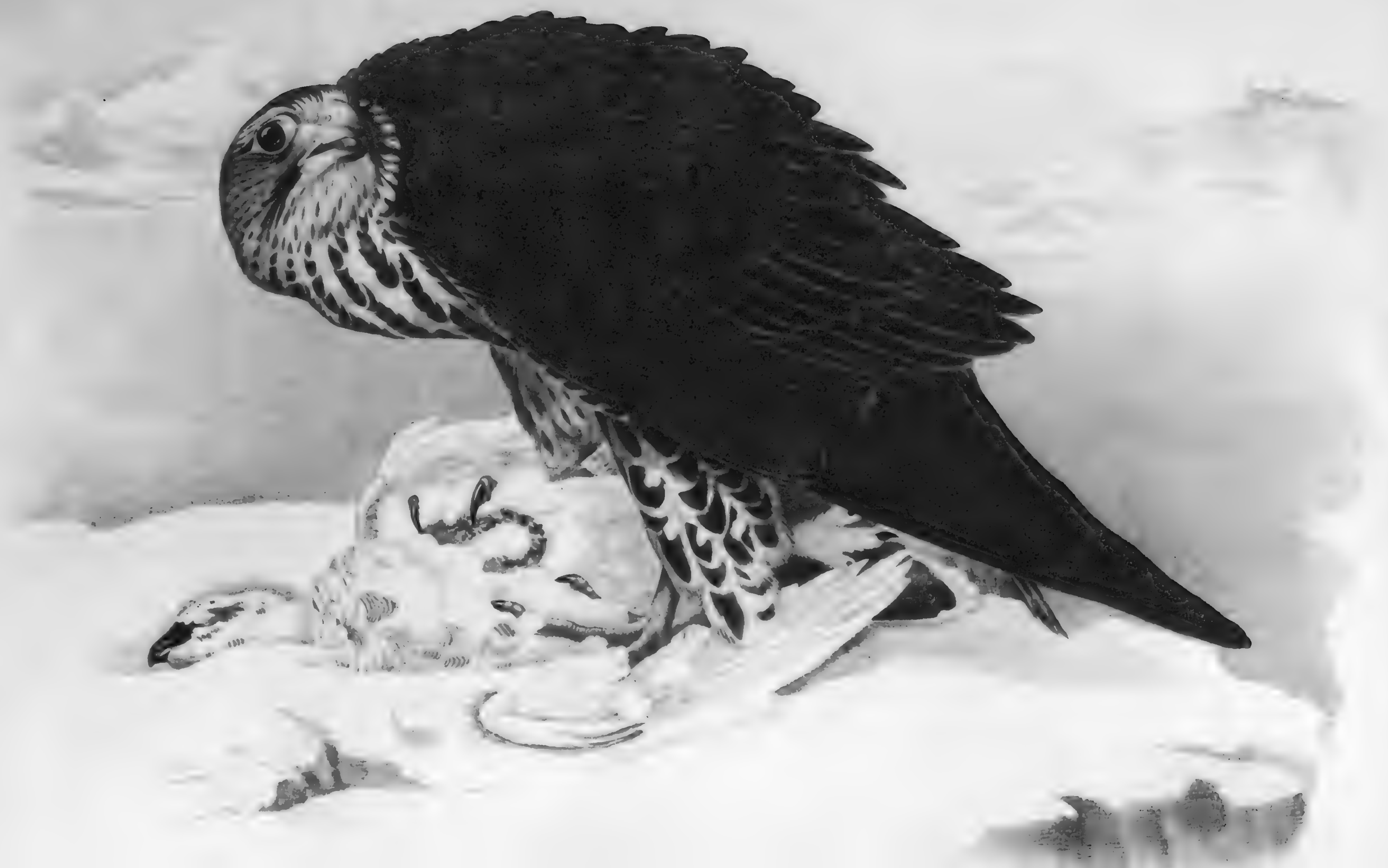


Figure 14. Preeminent among John Gould's illustrators, although contributing few pictures, was Joseph Wolf, the best ornithological draftsman of the 19th century and a noted animal artist. These pencil sketches (Blackcock, *Lyrurus tetrax*, and assorted mammals) are from an apparently unpublished collection in the Ralph Ellis Library at the University of Kansas.

Figure 15. Joseph Wolf's falcons were the finest raptors and among the finest birds delineated before Louis Agassiz Fuertes. Note the authentic, unstylized highlights in the eyes of this Gyrfalcon from Schlegel and Wulverhorst's immense *Traite de Fauconnerie*, 1844–1853.



Some Very Early Work

Insofar as our subject is concerned, the Renaissance was more notable for a new spirit of questioning authority than for its knowledge or the quality of illustration that accompanied the few books giving significant attention to birds. Three illustrated ornithologies, all of the late Renaissance, matter: those of Pierre Belon in France and Conrad Gesner in Switzerland, both 1555, and Ulysses Aldrovandi in Italy, 1599–1603 (3 volumes) [*27*]. These were illustrated with crude woodcuts by various workers, alike as primitive draftsmen, and of little skill as woodcutters (Figure 1).

Furnished with no more than crude stubs for perches or lumpy pedestals representing earth, these creatures, when not imaginary, can often scarcely be identified to order or family and few beyond the generic level. The confusion of the authors, of course, was equally great. While there are in these works rare un-Medieval flashes of observation and wonder, and the very act of encyclopedic exposition is decidedly Renaissance, the general level of observation of nature is inherited from the Dark Ages. One may appreciate the gulf between Art and bird art at this point by noting that by 1555 the world had already seen Leonardo, Raphael, both Holbeins, Michelangelo, and Titian.

Here and there, but outside of what we call ornithology, birds had already been rendered with far greater skill and closer observation even on Medieval wall tapestries. Those, and especially the sketchbooks of the little-known artist Giovannino de' Grassi (d. 1398) and the works of the well-known Antonio Pisanello (1395-ca. 1456), are justly praised [*28*]. Clark is correct that Pisanello's animals are more *accurate* than any which preceded them, but if he means to include wild birds when he says that they are more accurate "than most that were to follow," [*29*] we part company. If he has indeed seen much of what followed, then he and I must see birds in very different ways.

The Beginnings of Ornithology

Natural history may be said to begin with Francis Willughby (1635–1672) and John Ray (1627–1705), the first naturalists to make direct field and laboratory studies of birds. The illustrations of their great works (1676, 1678) [*30*] are a long stride toward ornithology if having little to do with art. Copperplate permitted much greater precision than the earlier woodcuts (Figure 2, 3) for rendering the anatomical detail necessary to the description and analysis of function. The birds have improved greatly in little over a century.

The ornithology of exploration and discovery took a great pioneering step forward a half century later with Mark Catesby (1679–1749). His *Natural History of Carolina, Florida, and the Bahama Islands* (1731–43), published in London, was the first of a long series of great folio volumes with hand-colored plates of birds and the first major natural history devoted to the New World by anyone who had been there. Artistic intent is clearly present and, aside from the few exceptions noted above, it contained the best living wild birds drawn to its time and, with no exceptions, the most dramatic (Figures 4, 5). If somewhat crude, they are large, colorful, and spirited. Catesby was also a dedicated botanist, and loving attention to floral details as an accompaniment to birds appears for the first time. Although mostly without "backgrounds," the birds occupy often elaborate two-dimensional environments. A number of ambitious folio works followed but none had comparable spirit and artistic quality for more than 50 years.

The most conspicuous improvement in perception of the bird for many years was achieved by the humble but solid English northcountryman Thomas Bewick (1753–1828), of Newcastle Upon Tyne, with an unpretentious little book in two volumes entitled *The History of British Birds* (there was a companion volume on "quadrupeds" = mammals) first published in 1797 (land birds) and 1804 (water birds). Modestly priced and sized, they were immensely popular and many editions followed.

Bewick's fame rests upon his unprecedented perfection of the art of wood engraving and the charming little landscapes that decorate his work as vignettes and "tail-pieces" to its accounts of animals. These accessory vignettes (Figure 6), especially, have delighted esthetes from Ruskin to Kenneth Clark. His birds, while somewhat unimaginative (nearly always shown in stiff side view), are related to simple environments and reveal a clear understanding, for their time, of what birds look like (Figure 7). One wonders, however, what Bewick's position in art history would be if he had omitted the non-zoological vignettes.

Very different was William Swainson (1789–1855), a sophisticated and eminent ornithologist who illustrated and lithographed his own *Zoological Illustrations* (London, 1820–1823) and *Ornithological Drawings* (London, 1834–1836). A contemporary of Audubon, Swainson early developed his skills independently. His bird drawing (Figures 8, 9) is advanced for its time; he had as good a grasp of basic bird anatomy as did Audubon, and was one of the first artists to show birds foreshortened and in motion. In drawing the avian eye and its highlights, he occasionally departed from the conventional pupil-splitting "V" of earlier workers and most later ones until Joseph Wolf began doing so in some of his pictures.

Audubon and the Great Years of Illustration

John James Audubon (1785–1851), whatever his real attainments, was a sort of P. T. Barnum in buckskin. He has been the subject of more literature [*31*] (good, bad, and indifferent), controversy, and general excitement than all other wildlife artists put together. Audubon is a legend, like the Yeti and its American vicariant Bigfoot, something which people evidently need.

His so-called elephant folio (actually broadsheet) *Birds of America* is itself the subject of a full-scale monograph [*32*]. Published between 1827 and 1838, the 435 handcolored aquatint copperplates of great delicacy, mostly by Robert Havell of London, are usually bound in four volumes. Except for the Gutenberg Bible, it has brought the highest prices of any book in history and is physically almost the largest. Reproductions may be found in several forms [*33*]. With John Bachman and aided by his sons Victor and John, he also dealt with American mammals.

The American art critic Thomas Craven [*34*] thought Audubon a major artist of world significance, describing all other bird painters, of whom he knew almost nothing, as "no more than taxidermists." Others (for instance Clark, as noted above) have not been so generous. Whatever his merits as an artist, and with much company I find them great, the recurrent ideas (principally held by people who know little or nothing of birds) that he was a close observer of nature and "ornithologically accurate" call for searching examination.

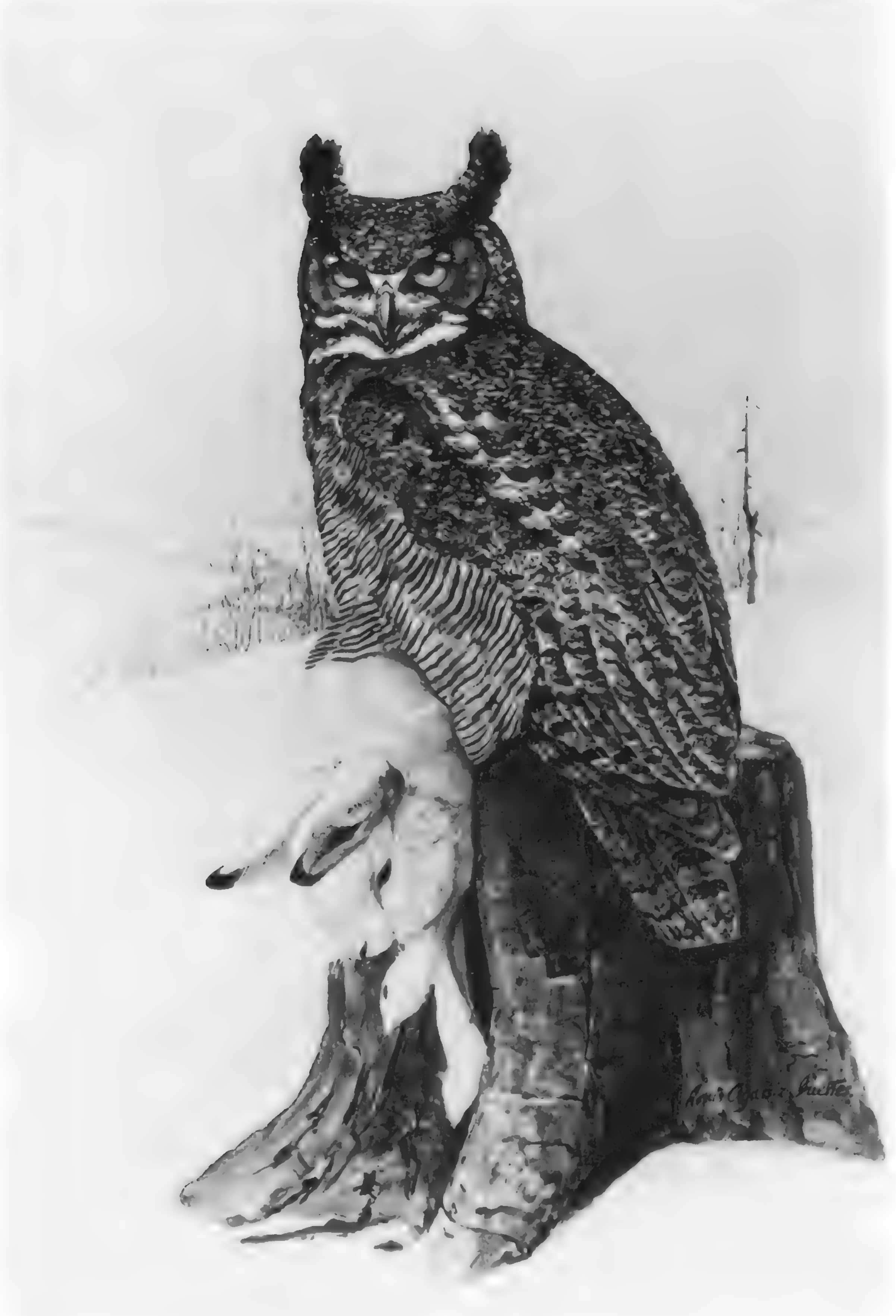


Figure 16. This loosely-executed, relaxed, superbly authentic Great Horned Owl reveals Louis Agassiz Fuertes' sure, strong grasp of essence and spirit. Reproduced from Marcham's work [*45*], courtesy of the Cornell Laboratory of Ornithology.

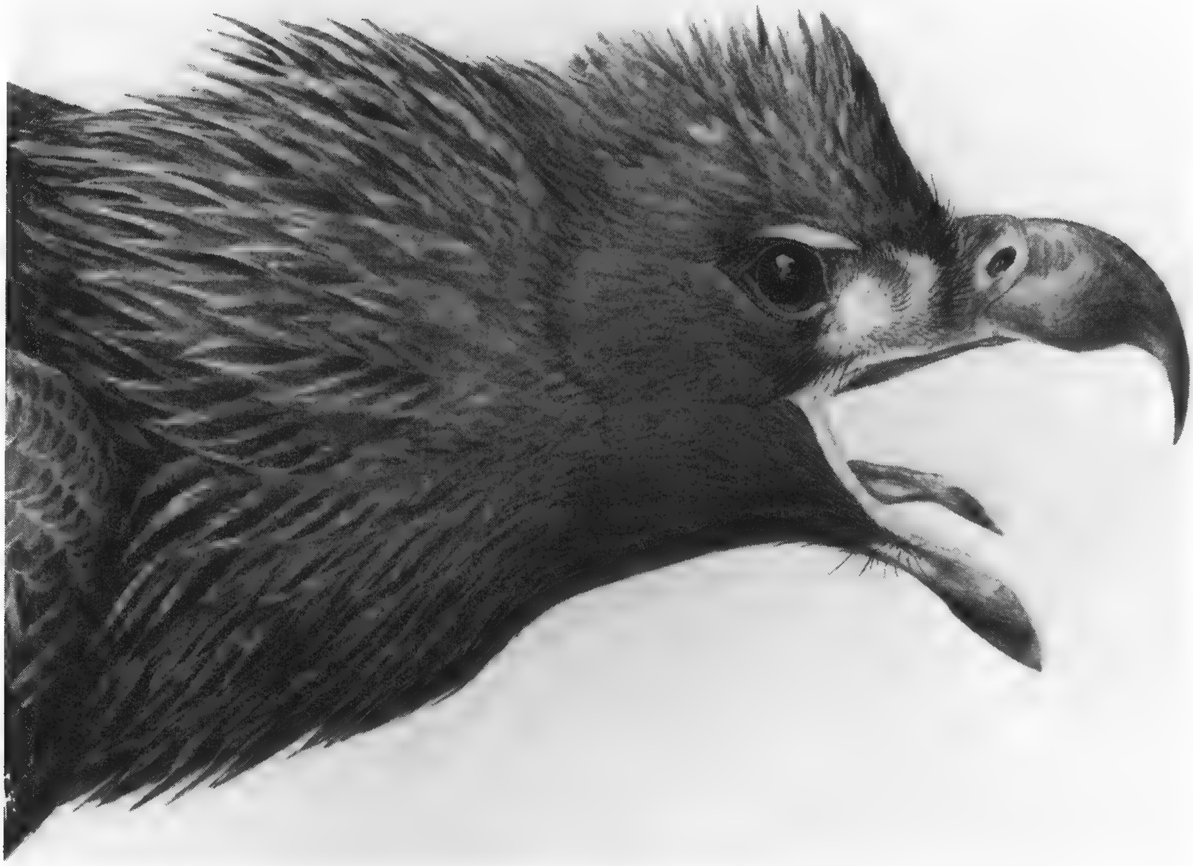


Figure 17. In this study of a young Bald Eagle, Louis Fuertes reveals his extraordinary capacity to make bird portraits live. Reproduced from Marcham's work [*45*], courtesy of the American Museum of Natural History.

Clark was actually right when he observed that Audubon's ornithological accuracy was little greater than that of Pisanello 400 years earlier; he erred in thinking that either was very accurate, either taxonomically (as defined above) or in that understanding of essence that comes only with deep knowledge.

How could Audubon have acquired such knowledge? He almost never drew from nature, or from the living bird. Even allowing that much of his early work was accidently burned, he drew fewer birds than any other major bird artist that I can think of, most species only once, and fewer than 100 of his works are major pieces of real devotion. By his own admission he had great trouble posing birds, impaling them on sharpened wires like any "mere taxidermist." Judging from many of the results, he was not a very good taxidermist. Few artists have gone nearly so far on so little actual application, but that, in itself, is an indication of genius.

Audubon's accuracy was an accuracy of surface and the spurious accuracy of detail, matters nevertheless that he handled with loving care and great delicacy. His immense detail, unlike that of his emulators, never intrudes and is acceptable because he was not a painter of light. Indeed, although he later developed some facility with oil, he was not in his best work a painter at all but a mixed media draftsman and tinter.

Except for the little known and unpublished Elizabeth Gwillim [*35*], his predecessor by many years, he was the first bird artist to relate many of his birds to ecologically appropriate backgrounds on a large scale. Yet he was in no major sense a landscapist. His landscape, often provided by other hands,

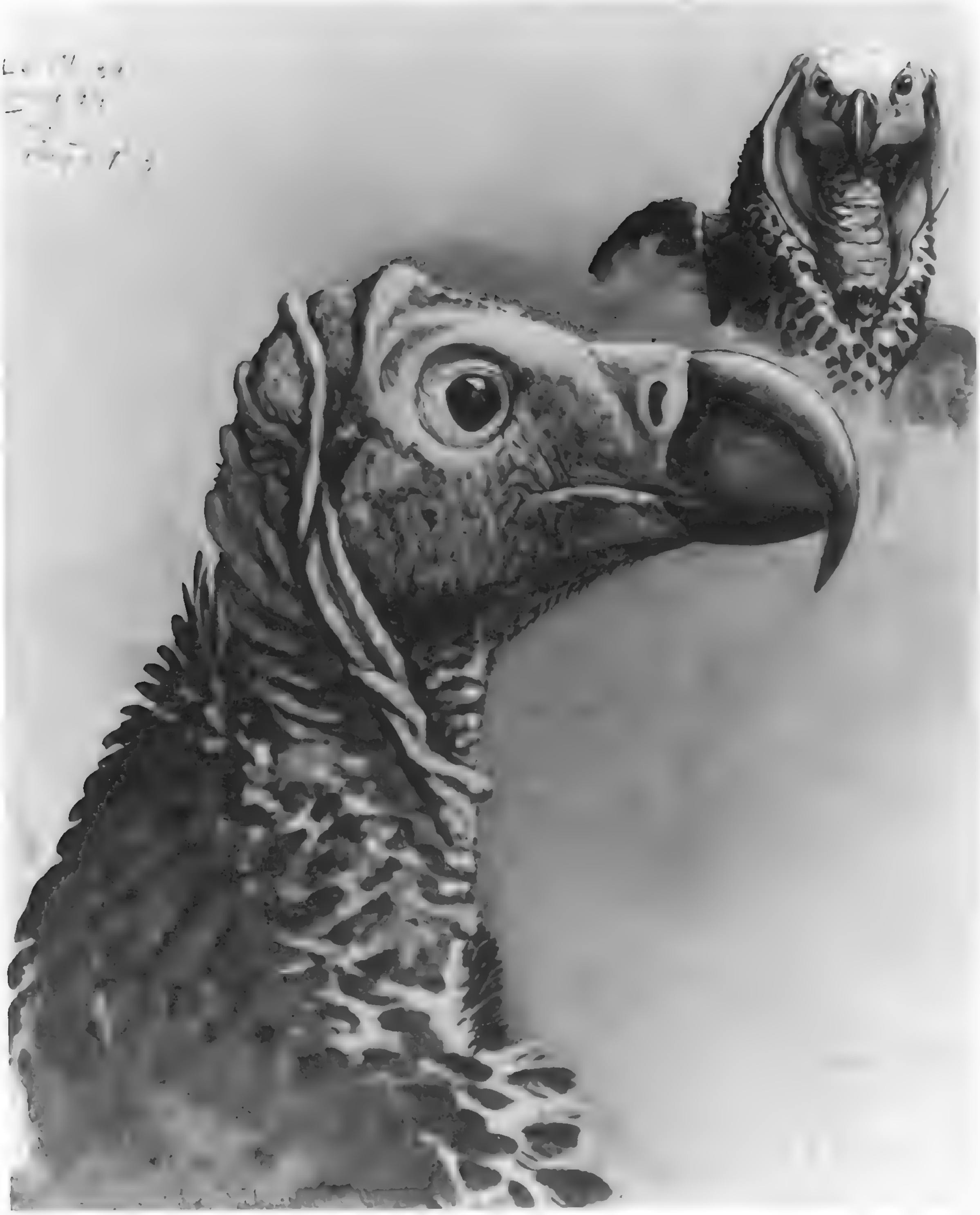


Figure 18. Among the many rapid field studies executed on Louis Fuertes' trip to Abyssinia is one of a Tawny Eagle, *Aquila rapax*, marked "(living bird)." Were it not so marked, it would be impossible to single it out from many of its companions based on the freshly collected specimen, for example this Lappet-faced Vulture, *Torgos tracheliotus*. Uniquely, Fuertes had the hard-won knowledge and innate sympathy to make birds live without benefit of motion or contrived position that Audubon could not approach with any amount of sharpened wires and that have eluded most of his successors with or without benefit of photography. Courtesy of Field Museum of Natural History.

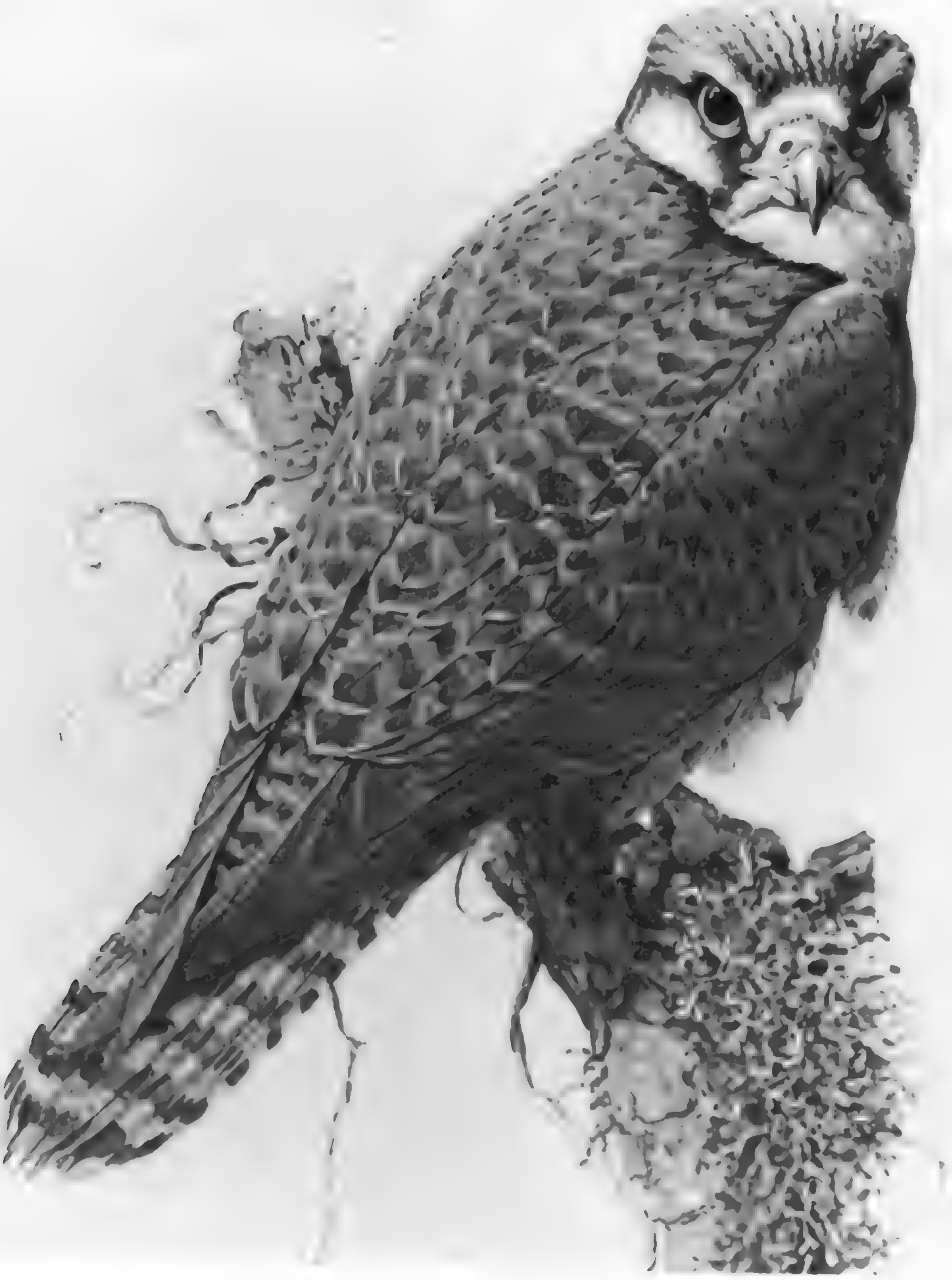


Figure 19. Abyssinian Lanner Falcon, *Falco biarmicus*, from the Fuertes Abyssinian album [*44*]. See also Figure 18. Courtesy of Field Museum of Natural History.

is backdrop unrelated to the all-important foreground and artistically unnecessary. His foreground vegetation is marvelously handled.

Audubon was a print maker, perhaps the best ever, and his strengths are in design (Figure 10), color, action, and texture. He was a supreme romantic, having much in common with his contemporary Eugène Delacroix. Audubon was fortunate in appearing at the height of the romantic period in painting which Delacroix, Géricault, and others had raised to immense popularity. As with Delacroix, his pictures have a tremendous energy. His birds (Figure 11), as I have argued at length [*36*], in facial expression and often attitude and context, suggest human rather than avian essences (cf. Delacroix's humanoid lions and horses).

I do not suggest, even given all of these things, that Audubon did not carry off some very fine birds — an astonishing achievement withal — superior as authentic birds to nearly everything that had gone before (I except Swainson). He brought wild birds and wilderness to the public mind as no one has before or since, Roger Tory Peterson not excluded (Peterson's justly famous field guides discovered a market that was already there; Audubon made it). He has naturally had many imitators, even unto the present day.

Audubon's effort remained the most flamboyant of the golden age of ornithological illustration that it ushered in. Literally hundreds of folio and quarto volumes [*37*] were devoted to the faunal works and taxonomic monographs of the nineteenth century, now increasingly to be found only in well-endowed state and university libraries. Production of these works was facilitated by stone lithography, which permitted easy rendition of various textures and allowed for precise delineation.

Their most industrious producer was John Gould (1804–1881) whose prodigious output, overall of considerable benefit to descriptive ornithology, has already been summarized.

The idea that Gould was a bird artist of consequence has still not entirely died out, even though great effort has been required to show that he did indeed draw one or two rough sketches of birds [*38*]. In fact, Gould employed and supervised a number of illustrators of varied competence and artistry: chiefly Elizabeth Gould (his short-lived wife), H. C. Richter, Edward Lear (a few pictures), and W. Hart. Among these, Richter and Hart were the most capable draftsmen of birds, the latter going on to serve the noted ornithologist Richard Bowdler Sharpe, Gould's literary and scientific executor.

The work of these people is representative of almost all the rest, pleasant but unobtrusive (hence attractive to interior decorators), adequate-to-good in presenting taxonomically acceptable birds amid attractive floral furniture and sometimes before pleasant and reasonably appropriate backgrounds (Figures 12, 13). There it ends. Viewed day after day, I can testify after hundreds of days at the job, these works have a sameness and monotony, a lack of spirit, that quickly palls into boredom.

There is at least one conspicuous exception. Another artist who worked briefly for Gould was Joseph Wolf (1820–1899), who stands totally apart from all the rest in his grasp of the anatomy, facial expressions, and essential construction and attitudes of birds (Figure 14). He was unsurpassed in these matters until Fuertes. One of the truly great animal artists, he had also a superior capacity for picture making (in which among his predecessors only Audubon excels him), and a unique skill at picture finish, or quality, defined as physical attractiveness of surface.

Wolf executed the finest falcons to his time for Hermann Schlegel and V. van Wulverhorst [*39*] (Figure 15). Above all in elegance stands his glorious work for D. G. Elliot's two-volume *A Monograph of the Phasianidae* (1870–1872), the most beautiful of all 19th century ornithological monographs save Audubon's and the most accurately illustrated of any in terms of avian essence (Plate 1).

Fuertes and the Modern Bird Artists

Infected with the enthusiasm of Audubon, but with a very different eye, Louis Agassiz Fuertes (1874–1927) [*40*] probably possessed the most thor-

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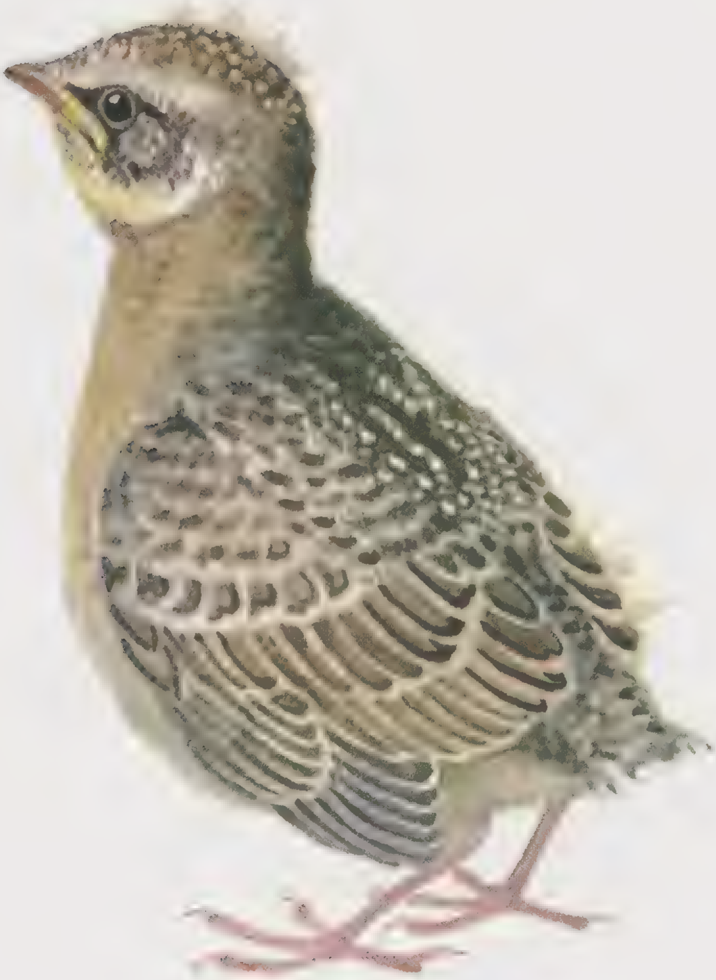
Plate 2. A young Horned Lark, *Eremophila alpestris*, here reveals George Miksch Sutton's well known sensitivity in the portrayal of downy and juvenal-plumaged birds, usually from life. Reproduced for the first time, by courtesy of the artist.



ough understanding of birds of any artist of any kind to the present time, excepting only Liljefors, who was his equal or even superior with eagles and large water birds.

This is his unique gift and total contribution. It is unjust, if not tragic, that only a comparatively few ornithologists and bird painters are adequately equipped for its full appreciation. More tragic, however much the gain to ornithology, is that Fuertes was required to spend most of his far too short life making a living by illustrating the many works — some 35 in all — for which his unrivalled skills made him the servant of choice.

Even in this task he was constantly pushed and pulled. He was discovered for ornithology by the great Elliott Coues, his early champion and mentor, and passed on to Frank M. Chapman. Fortunately he came early, also, under the kindly tutelage of the noted portrait painter and landscapist Abbott Thayer. As ornithologists were urging him to emphasize birds and eliminate the shadows and highlights that distort local color and obscure taxonomic characters, Thayer (with his brother Gerald the discoverer of "countershading" in nature) was urging him to make them less conspicuous and to emphasize the play of light and shadow. Never more than a barely adequate landscapist and with recurrent problems in composition (he had little time to master such things), he found his forte in portraiture and studies where little landscape was required (Figures 16, 17).

Even for artistically serious efforts at these things he was allowed little time. Occasionally he forced the issue. Examples are found in the superb "Prairie Falcon of Pyramid Lake, Nevada," one of the great bird paintings of all time (even the landscape is good) [*41*], reproduced in black and white in the *Birds of New Mexico* [*42*], and in its equal, the majestic, supremely appreciated "Duck Hawk of Mount Tom" that far exceeds in artistic importance all the other work in the *Birds of Massachusetts* [*43*] combined.

The further pinnacles to which he might have risen with longer life are suggested by the marvelous field portraits [*44*], made for his own pleasure alone, on his 1926 trip to Abyssinia with a Chicago Field Museum expedition (Figures 18, 19). There is nothing like them in all bird art.

I have heard the suggestion, and I agree, that emulation of Fuertes long had a deadening effect on American bird painting. It may account for the much greater freshness and variety, at least until recently, of European efforts where no such overpowering influence was felt.

A flying Sharp-shinned Hawk in the small collection of Church & Dwight Company, Inc. [*1*], which unfortunately could not be obtained for reproduction here, is one of Fuertes' truly great accomplishments and has never been published. It is a *tour de force* in its demonstrated knowledge of what can scarcely be seen long enough for analysis. As Frederic Remington did not need Muybridge's camera to know how a horse runs, so Fuertes required no stroboscopic flash.

Much of Fuertes' original work can be seen at the Cornell Laboratory of Ornithology, the bird department of the American Museum of Natural History, and at the Philadelphia Academy of Natural Sciences [*45*].

Fuertes had several extremely prolific contemporaries, the most notable in North America being Major Allan Brooks (1869–1946), a British Columbian of early promise who foundered in trite, syrupy puerility under the burdens of excessive illustration (20 works). Several equally or more productive Europeans, inheritors of the tradition if not the genius of Wolf, were stronger illustrators than Major Brooks.

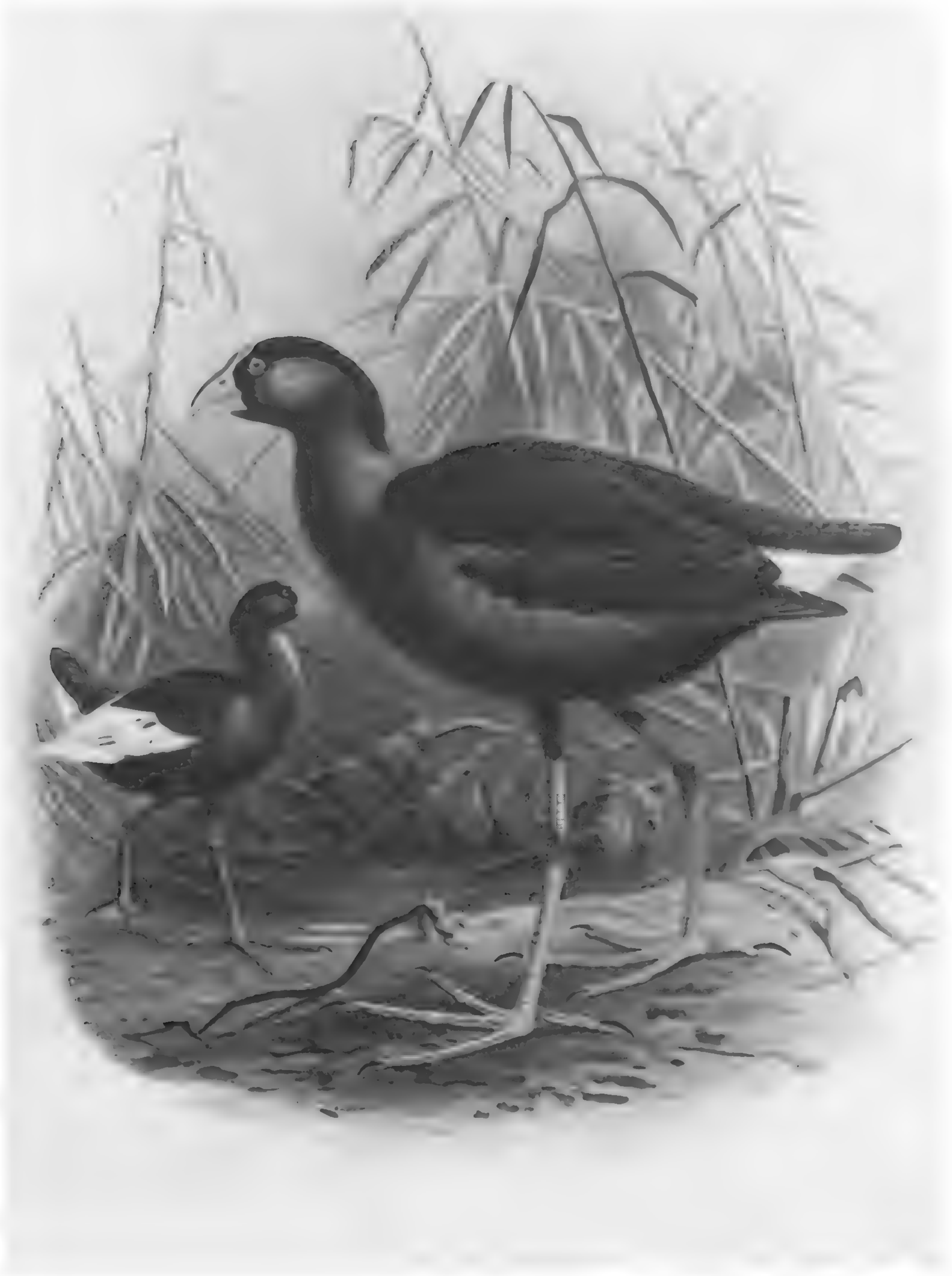


Figure 20. Most prolific of Fuertes' approximate contemporaries, indeed of all bird artists, was J. G. Keulemans, of whose work this figure from Sir Walter Buller's *A History of the Birds of New Zealand*, second edition, 1887–1888, is typical.

Chief among these were the Dutchman J. G. Keulemans (1842–1912), the Dane Henrik Grönvold (1858–1940), and Englishmen George E. Lodge (1860–1954) and Archibald Thorburn (1860–1935). Respectively, they illustrated all or part of at least 65, 45, 20, and 17 works (figures from Nissen), the first two being the most prolific ornithological illustrators in history.

Keulemans, though exemplary in taxonomic accuracy, was the least

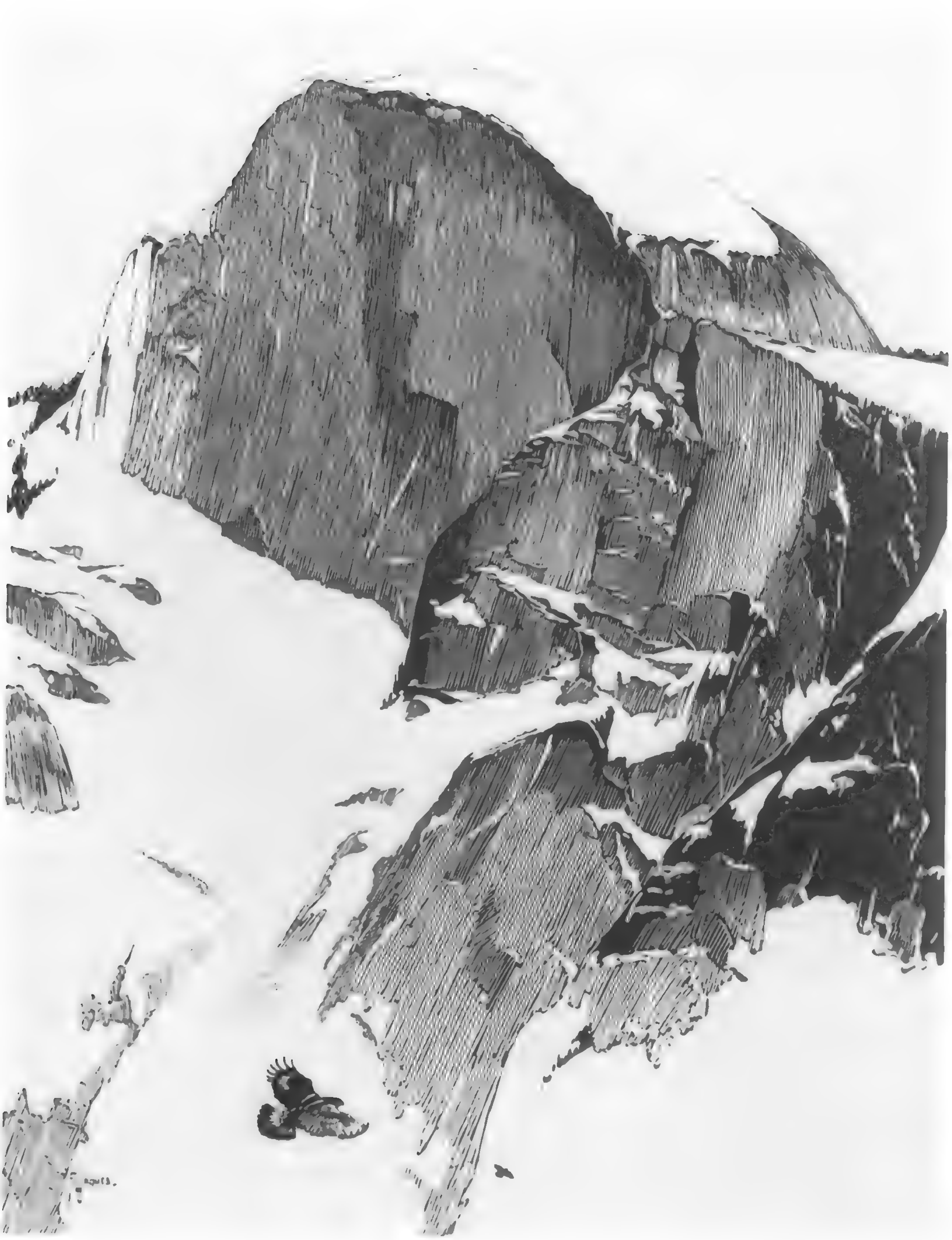


Figure 21. Francis Lee Jaques is as well known for his powerful and carefully composed scratchboard black and whites as for his more ambitious paintings and diorama backgrounds. This golden eagle before a cirque is from *F. L. Jaques, Artist of the Wilderness World* [47], reproduced by courtesy of the Nature Conservancy.

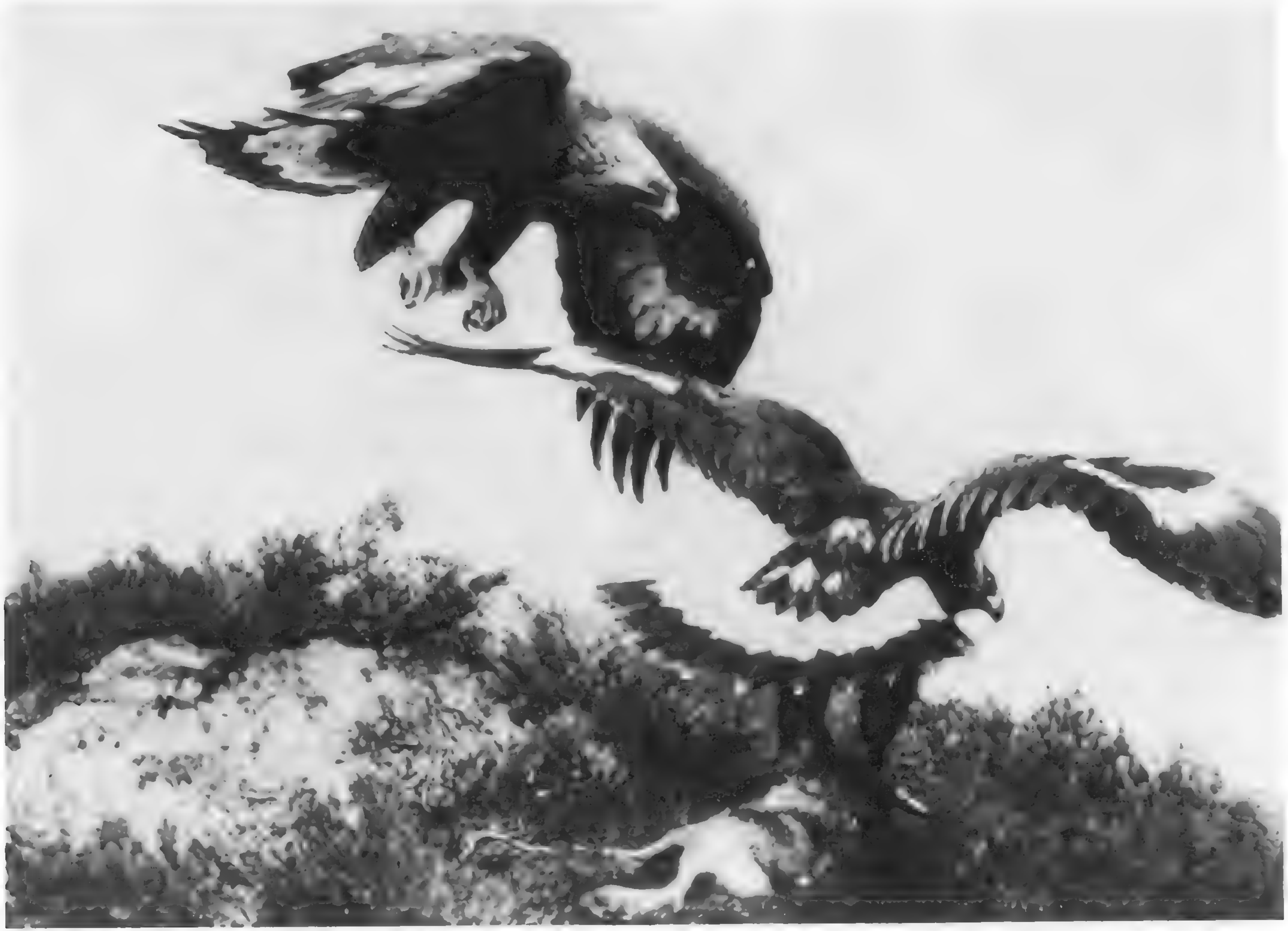


Figure 22. The immense power, control, and penetrating vision of Bruno Liljefors is nowhere better shown than in his large studies of raptors and sea birds. These Golden Eagles, *Aquila chrysaetos*, are an outstanding example.

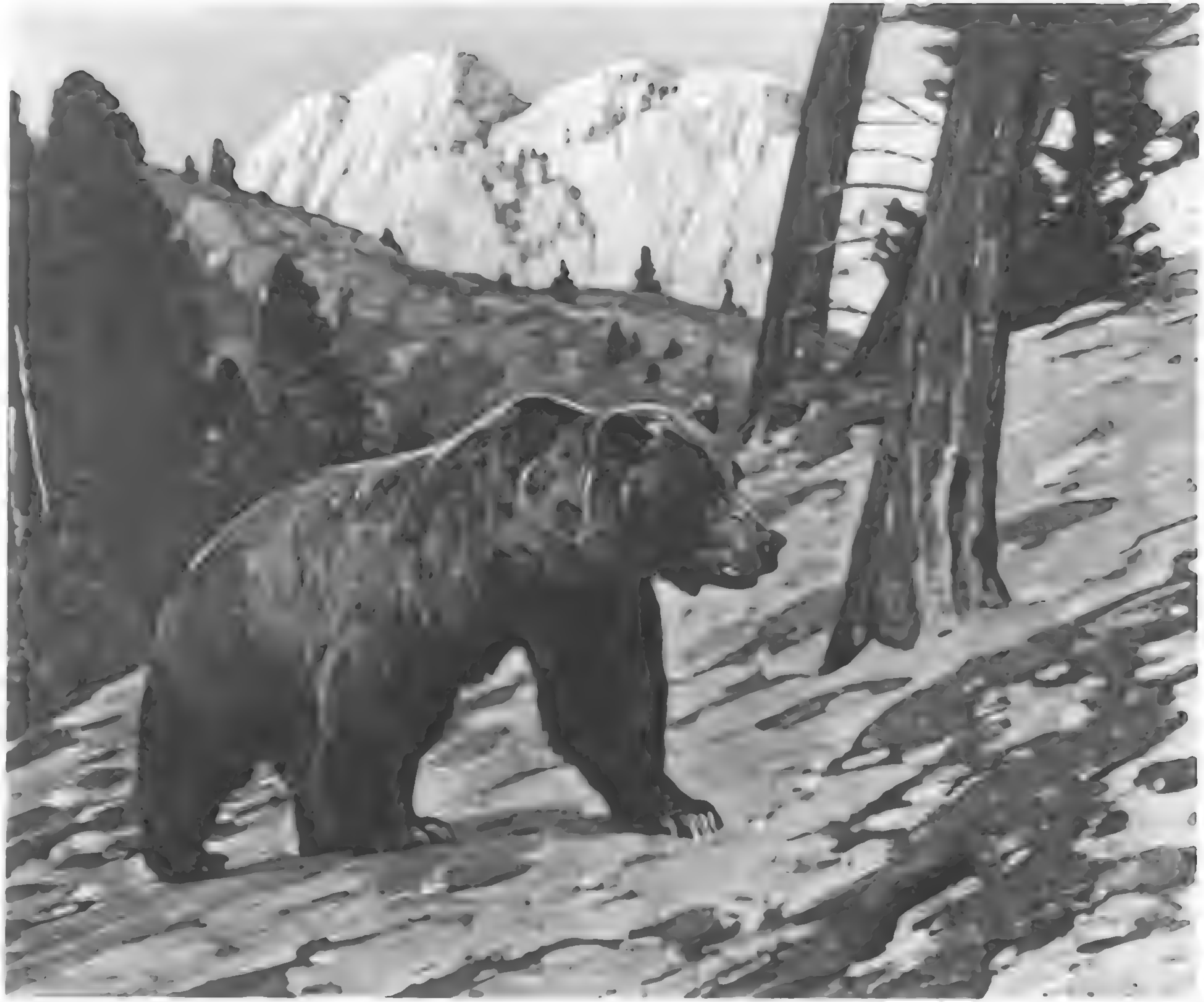


Figure 23. Striding morosely up a soggy slope amid the melting snow of spring, one of Carl Rungius's many grizzlies *(Ursus arctos)* is the focal point of a superb example of this artist's power to convey the mood and ecological essence of awesome landscapes inhabited by superbly appreciated creatures of equal grandeur. Rungius's large oils must be seen to be fully appreciated

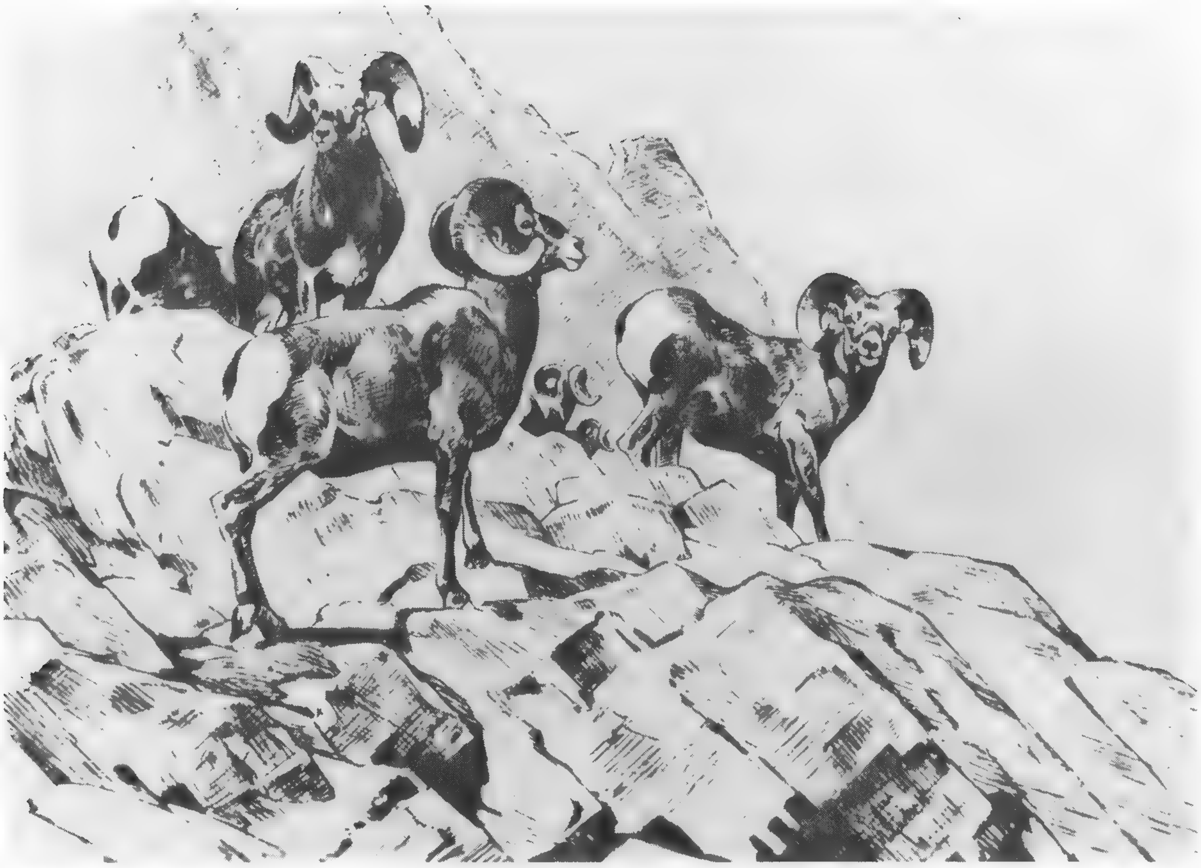


Figure 24. A drypoint of Rocky Mountain sheep, by Carl Rungius. See text. Rungius's compositions are always carefully balanced, strong, and very patiently thought out.

spirited, producing detailed, but flat and lifeless, colored diagrams. His work for the second edition (1887–1888) of Buller's monograph on the birds of New Zealand is some of his very best work (Figure 20). Grönvold's birds were more colorful and lively, but somewhat stylized. Lodge's pictures lean to fussiness and his birds to fuzziness, lacking strength and conviction. He painted to a very ripe old age and his late work should not be held against him. Thorburn was the best of the lot artistically; at least he knew how to make a pretty picture (too pretty) and his feeling for texture and finish was highly developed [*46*]. He drew both mammals and birds. The latter lack all of the strength and most of the understanding of Fuertes.

Two artists whose careers had been launched before 1927 deserve mention but pose a problem. It would be unfair to judge them by their early work, yet the bulk of their best extends far to this side of the 50-year barrier adopted as a standard for perspective. One is Francis Lee Jaques (1887–1969), a painter in the full sense and a landscapist well-known and popular through his many diorama backgrounds, oil paintings (especially of wildfowl), and scratchboards [*47*] (Figure 21). The other is George Miksch Sutton (b. 1898), still painting and the clear elder statesman of American bird art. An early protégé of Louis Fuertes, Sutton eschewed the pathway of emulation, establishing several of his own approaches. He is perhaps best known for his favorite subjects: delicate small birds often in miniature landscapes and young birds (Plate 2). These sensitive portraits in great number (often showing little-known or previously unknown plumages) have provided a very significant contribution to ornithology as well as much pleasure [*48*].

These many wildlife artists kept alive for centuries the spirit of curiosity

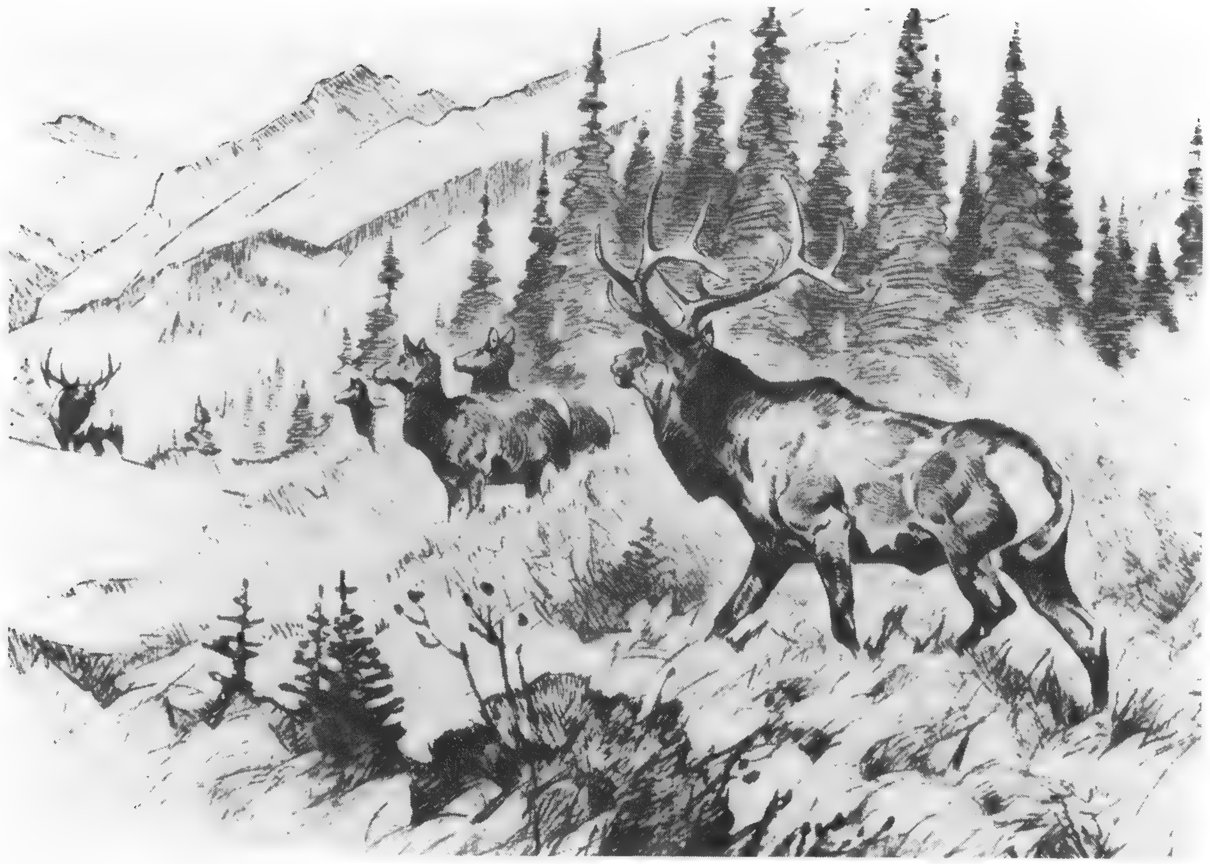


Figure 25. Drypoint by Carl Rungius of wapiti, or elk. Entitled "Challenged," the composition also appears in one of the artist's major paintings, another example of his care with both composition and animals.

and reverence for wild things and wild nature that had otherwise almost vanished from Art.

Some Painters

Peripheral to formal natural history were four artists of uncommon ability, born within 15 years: Richard B. L. Friese (1854–1918), Bruno Liljefors (1860–1939), Friedrich Karl Wilhelm Kuhnert (1865–1926), and Carl Rungius (1869–1959).

All received considerable formal grounding in art and were sufficiently motivated to overcome various obstacles in the way of making their life work the painting of animals. Liljefors in Sweden and Friese and Kuhnert in Germany achieved widespread popularity and artistic recognition in their countries at a time when animals were acceptable, even popular, subjects in art. The work of Friese, whom Rungius generously regarded as the greatest of large mammal painters [*49*], hangs in many European galleries and was popular with Kaiser Wilhelm II. Kuhnert's work, including some very well painted birds, may be seen in reproduction in a few works, rare in this country, for which he served as illustrator [*50*]. Rungius, coming early to the United States (he once told Colonel Theodore Roosevelt that he was "always an American") [*51*], established deeper acquaintance with wilderness than any of them but was forced to swim against very different currents in art.

Bruno Liljefors

Considered by many the greatest of all wildlife painters, a conclusion that I would contest only with reservations to follow, Liljefors is one of

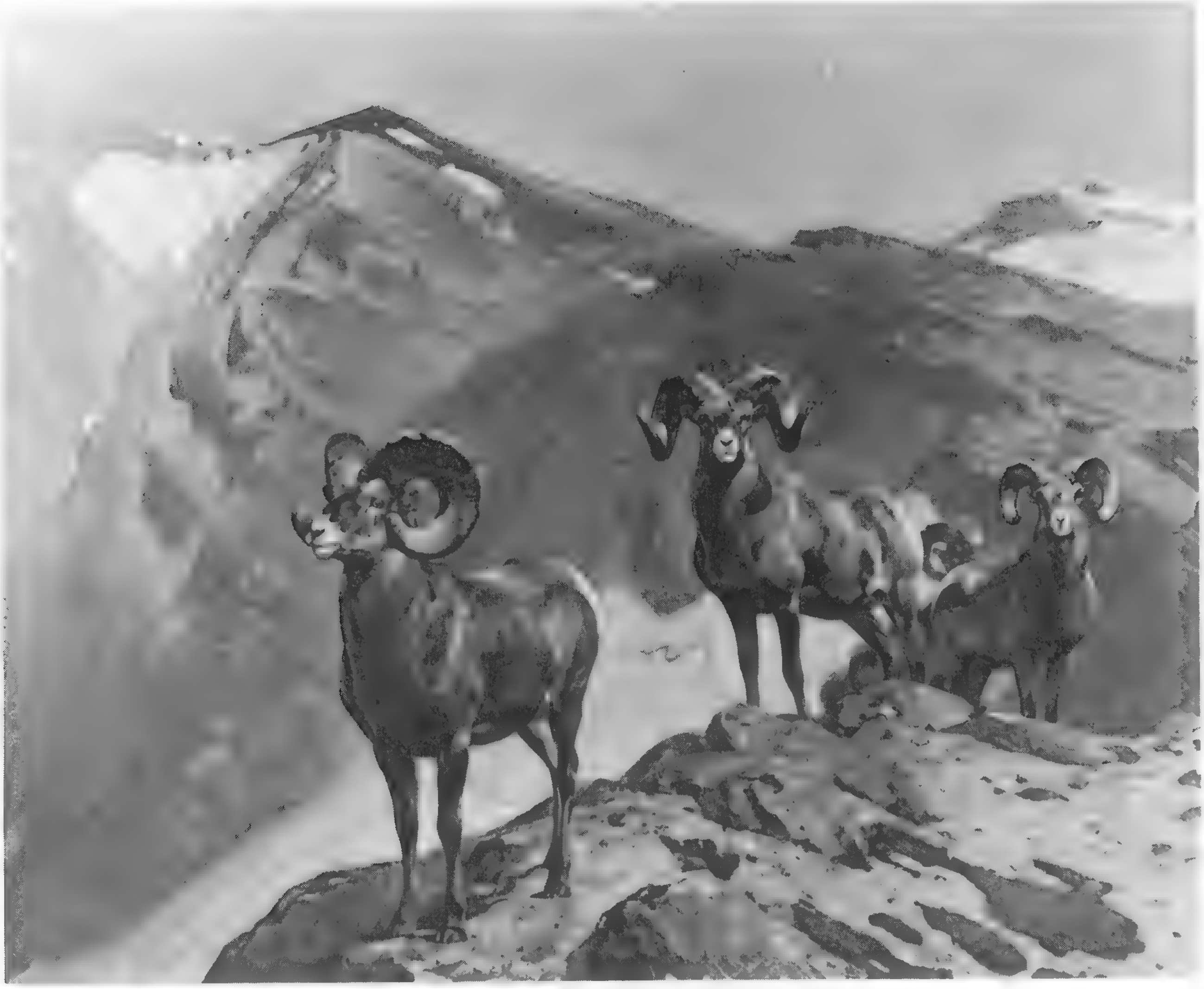


Figure 26. This painting of Rocky Mountain sheep by Carl Rungius is one of his many devoted to this species, all grand.

Sweden's most beloved artists [52]. Sweden has been the least afflicted of any western country by prejudice against nature in art. A result of this is that almost none of his original work has been exported. Much of it may be seen in the Thiel Gallery in Stockholm. Those without access to the few hard-to-get books devoted to it [53] may thank the journal *Audubon* and its picture editor Martha Hill, respectively, for recent reproductions (very revealing despite deficiencies in color) and a sympathetic vignette of the artist [54].

Competently trained at the Royal Academy, Liljefors had humor (in early hard times he was a successful cartoonist), intensity, and great range. He could be gentle and searching in his rare portraits of family and friends, subtle and exquisitely sensitive in treatment of dark forest or dew-wetted grass or a bit of sedge marsh and snipe. He was uncanny with wild-eyed, hunting tabbies. Above all he excelled in painting the sculptured hammered iron of wind-scoured ocean and its totally indigenous, highly simplified (sometimes to the point of abstraction) eiders, loons, and sea-eagles. Some of his Golden Eagles (see Figure 22) are the greatest ever painted, perfectly perceived in broad, true, economical strokes which give the impression of great detail where, in fact, there is very little; these eagles float in precise, weightless balance on wind that is felt. Very much a painter of light, he was, especially in his later work, inclined towards impressionism. But his is always a focused impressionism, not without line, blurred only where blurring serves truth or eliminates the non-essential. A devoted hunter with excep-

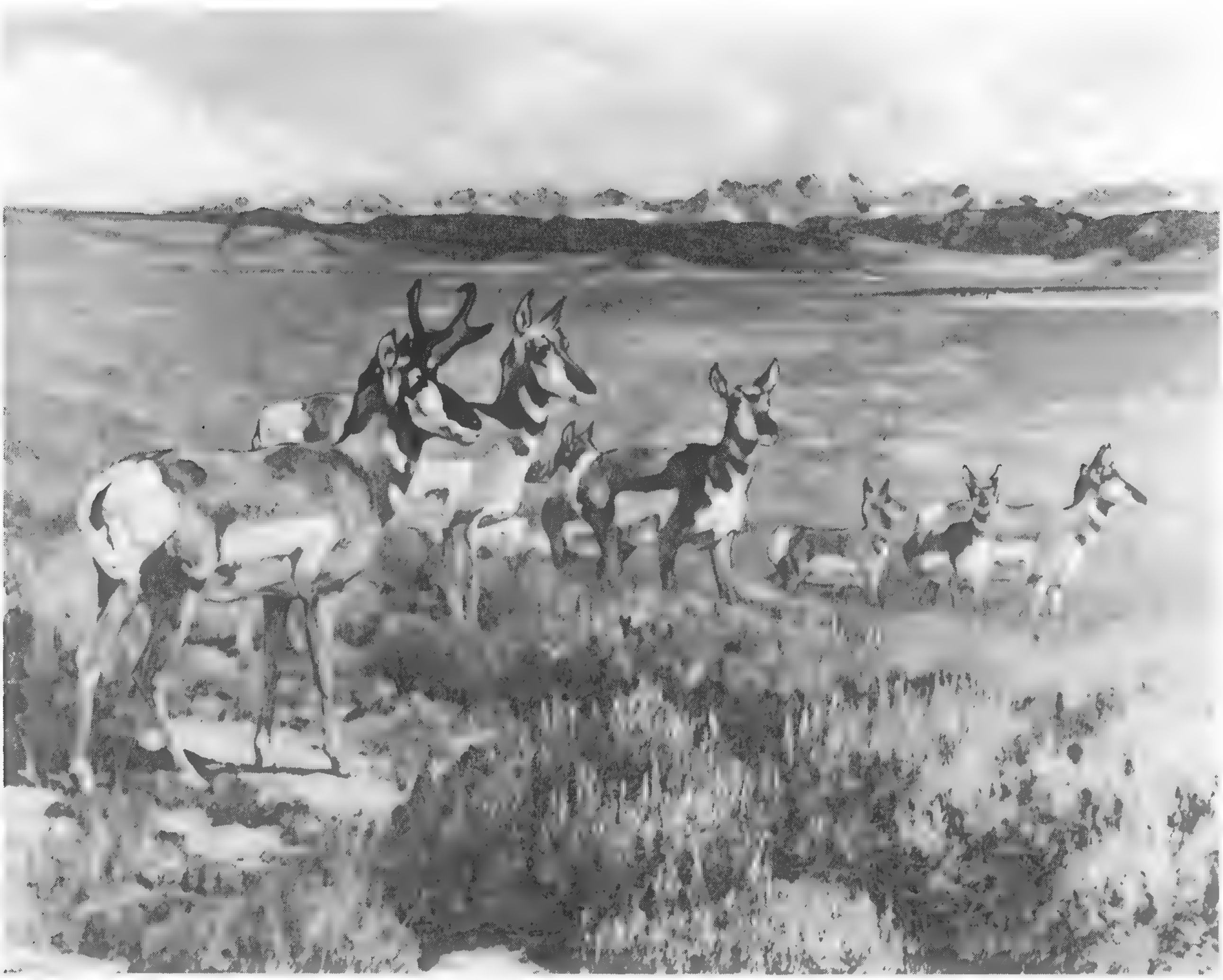


Figure 27. The sweep of the Wyoming plains and the majesty of the Wind River Range in the background here complement Carl Rungius's superb pronghorns.

tional powers of observation, he *knew* what he painted. His composition became simpler with time. His landscape, more often intimate than sweeping, envelops rather than serves the animal subjects which are almost always present. It is true wild landscape, keenly perceived but rarely for its own sake alone.

Carl Rungius

Quite different was Carl Rungius in everything save greatness. He never painted birds, so far as I know, and mammals rarely interested him unless large enough to occupy an appreciable expanse of horizon at 20 meters.

Some of his paintings were well reproduced in a fine book by William Schaldach now very hard to obtain [55]. Others were well reproduced about 25 years ago in a calendar whose source I cannot recall. Some of the originals not in private hands may be seen at the Bronx headquarters of the New York Zoological Society, at Jackson Lake Lodge in Grand Teton National Park, and at the Glenbow-Alberta Institute, Edmonton [56].

Trained in Berlin schools of art, Rungius came in 1894 to the United States in search of wild nature and the big game that attracted him. First he painted in eastern Canada, later in still frontier Wyoming and in the Yukon. Early a naturalized U.S. citizen, he established in time lifelong studios in Banff, Alberta, and New York, doing his tireless field work through the Canadian Rockies with pack train and rifle in the summer, his studio painting in the winter. He was a supreme naturalist, expert woodsman, and consummate big game hunter into his mid-70's. He knew at first hand moose, caribou, sheep, goats, and grizzlies as no man has before or since. His grizzlies at massive ease (Figure 23) are infinitely more awe-inspiring than the aroused ones of lesser painters.

Early in his career Rungius was surprised when his canvases were frequently refused by major art shows. "It is the animals, Rungius," his artist friends assured him, "take them out." He took them out, and his superb landscapes of the Canadian Rockies, unlike any other western American landscape painted, quickly won recognition, numerous prizes (some even *with* animals), and full membership in the National Academy of Design by 1920, he being the only painter of wildlife so recognized.

Having made his point, and with many waiting commissions from the affluent big game hunters who supported him well, Rungius happily returned to his animals, organic elements in landscapes as great as ever.

Like Kuhnert, Rungius was skilled at drypoint and often planned or repeated his paintings in this medium (Figures 24, 25). He was a tireless and rapid sketcher in the field in both oil and pencil (his drawing both sure and pleasing) and the first-hand data thus accumulated were vast.

Early Rungius shows no trace of it, but even before the 1920's he seems to have been influenced (as few were not) by impressionism. He never became an impressionist, however. With the capacity of all great artists to assimilate without emulating, he superimposed impressionist light and color upon careful draftsmanship and painstakingly constructed landscape of great architectural solidity and geological integrity (Figures 26, 27). Coincidentally or not, there is something of Cezanne in his reduction of authentic landforms to angular, repeated, somewhat rectangular balancing masses with which his great mammals conform and interact. His is never the lightning action picture of Liljefors, but a carefully constructed, orchestrated whole of profound ecological truth. He painted a window to the wild grandeur of the northwest and its greatest creatures not even approached in American art and with few parallels anywhere.

Epilogue

The existence of such terms as wildlife art (of which Carl Rungius would have no part) is historical fact. We have seen some reasons for this. For my part, I should like to see these terms become anachronistic.

This seems unlikely until those artists whose strongest stimulation comes from wild nature and the beauty of animals cease to huddle apart in separate enclaves and to paint solely for the satisfaction of specialized and too frequently undemanding audiences. Studies of insular biology tell us that island populations fare poorly in competition with their more rigorously selected mainland counterparts. From competition comes strength.

Conversely, terms such as wildlife art will persist also until the barriers to recognition are shattered and subject matter is truly ruled out of consideration. Surely such education will not be accomplished by the withdrawal of naturalists from the councils of man and serious painters of nature from the councils of Art. At no time in history has more attention been focused upon the true meanings of man's relations to the natural world. The attitudes toward this world that led to man's present environmental predicament are fundamentally the same as those that caused Art to turn away from nature in the first place. On every hand they are being reexamined.

Acknowledgments

For various assistance I thank J. J. Hickey, M. A. Jenkinson (helpful reading of MS), Alexandra Mason and William Mitchell (loan of works in the Ellis Collection, University of Kansas Libraries), R. S. Palmer, Larry Schwarm (photography), George Miksch Sutton, and Margaret Wilson. For information about or permission to reproduce various works I thank William Comstock (of Harper and Row), the American Museum of Natural History, and the Cornell Laboratory of Ornithology (L. A. Fuertes), the Field Museum of Natural History (L. A. Fuertes), Joan-Elisse Carpentier (of Doubleday & Co.), Geoffrey S. Barnard (F. L. Jaques; courtesy of the Nature Conservancy from F. P. Jaques, *Francis Lee Jaques, Artist of the Wilderness World,* Doubleday & Co., 1973), Richard Lattis (of the New York Zoological Society), David A. E. Spalding, of the Provincial Museum of Alberta, and Jeffrey Spaulding, of the Glenbow Alberta Institute, Calgary (Carl Rungius).

Notes

1. Made available through the courtesy of the Arm & Hammer Division of Church & Dwight Co., Inc., New York.

2. Some of the many relationships involved have also been considered by D. R. Eckelberry (*Living Bird,* 2:69–82, 1963).

3. This rhetorical question has also been asked by G. M. Sutton (*Living Bird,* 1:73, 1962) and D. R. Eckelberry (*Living Bird,* 2:69, 1963).

4. *Introduction to the History of Science,* Vol. 1. Williams and Wilkins, Baltimore, 1927, page 4.

5. William Morrow and Company, New York, 1977.

6. C. Nissen. *Die illustrierten Vogelbücher,* Hiersemann Verlag, Stuttgart, 1953. Estimate of entries marked "Z" (for draftsman or painter) in list of artists.

7. Thieme and Bekker's monumental *Kunstlerlexikon* in many volumes (1907–1950); also the similar work in French by Bénézit *et al.*

8. The blame for overall quality is not solely the artists'. Publishers often base their selections less upon merit than upon what they think will sell. If the discriminating are unharmed, painters and purchasers alike are thus deprived.

9. "An Essay on Criticism," lines 293–296, 1711. Quoted from *Oxford Dictionary of Quotations,* Second edition. Oxford Univ. Press, London, 1955, page 382.

10. I could scarcely have made this point better than did Paul Richard, art critic for *The Washington Post* (February 1, 1980), reviewing, since my lines were written, selections from one of the Wausau bird art shows mentioned elsewhere herein:

> [Birds] stink, if truth be told; they peck at one another. … [They] are beautiful, but they are not friendly. Their scaly legs are sinister. Beneath their lovely plumage they resemble snakes with wings.

Richard defends other parts of my thesis also:

> Bird painters take the greatest pains and use the smallest brushes to assure that each beak they paint, each feather's barb and barbule, each claw and beady eye, is portrayed just so.

> The pictures [they] produce in such astounding numbers are astoundingly conventional ... both admirable and awful. The craftsmanship is splendid, but the sameness of these pictures begins to numb the mind.
>
> The painting of birds — like the spinning of a prayer wheel, the saying of the rosary or the muttering of mantras — is an act of tedious prayer.
>
> Only rarely do these bird works recall other sorts of painting... but it's nice to see that [a few of the artists have] looked at pictures that are not bird art.

11. I am indebted for this analogy to a useful essay by Bernard Myers. *How to Look at Art*, Vol. 10 of *The Book of Art*, Grolier, New York, 1965, page 92.

12. Eckelberry (paper cited in note 2) calls this "intellectual realism." I am not here concerned with the possible utility of this term, and its relatives, in analytical criticism, or with the validity of the states of mind that they represent. As the self-conscious equipment of painters, however, they would strike me as vaguely alarming if, as Kenneth Clark suggests (*Landscape Painting*, Charles Scribner's Sons, New York, 1950, page 94), "decadence in all of the arts manifests itself by the means becoming the end."

13. K. Clark. *Landscape Painting*, Charles Scribner's Sons, New York, 1950, page 1.

14. Ibid., page 16.

15. Ibid., page 78.

16. As quoted by M. S. Haverstock. *An American Bestiary*, Harry N. Abrams, Inc., New York, 1979, page 89. Typical of its genre, this work contains many zoological errors.

17. For reproductions see: M. S. Haverstock, *An American Bestiary*, Harry N. Abrams, Inc., New York, 1979, page 85; P. J. Broder, *Great Paintings of the Old American West*, Crown Publishers Inc., New York, 1979, pages 48–49; P. A. Rossi and D. C. Hunt, *The Art of the Old West*, Alfred A. Knopf Inc., New York, [1971?] pages 194–195.

18. For many reproductions see publications cited in previous note.

19. This attitude is recurrent in literature as well as in painting while its opposite is uncommon. Joseph Conrad found only nameless dread in the jungles of the Congo (*The Heart of Darkness*), while in *The Green Hills of Africa* Ernest Hemingway wrote with brimming love and clear perception.

20. K. Clark, work cited in note 12, page 142. In discussing the turning away of Art from nature (i.e., landscape), among other reasons for it Clark says that earlier art was "based on a living idea, that nature was friendly and harmonious. Science has taught us that nature is the reverse; and we shall not recover our confidence in her until we have learnt or forgotten infinitely more than we know at present."

21. I do not wish to give the impression that I live in a vacuum. The dim prospects for wilderness and a harmonious, even workable, relationship between industralized man and nature, for those who have the stomach to read them, have been examined by many, a notable example being R. E. Dasmann (*The Last Horizon*, Collier Books, New York, 1963). So much greater the contribution of the few painters of wilderness.

22. For excellent text and reproductions see L. Goodrich. *Winslow Homer*, Whitney Museum of American Art, New York, 1973.

23. Houghton Mifflin Co., Boston, 1955, pages 103–104.

24. M. S. Haverstock. *An American Bestiary*, Harry N. Abrams, Inc., New York, 1979. A delightful surprise in this fascinating book is the lovely painting of alligators by John Singer Sargent, famous for his society beauties. Perhaps he sensed a sinister kinship between the seemingly disparate subjects.

25. J. Anker. *Bird Books and Bird Art*, Levin and Munksgaard, Copenhagen, 1938.

26. C. Nissen. *Die illustrierten Vogelbücher*, Hiersemann Verlag, Stuttgart, 1953.

27. Respectively: *L'histoire de la Nature des Oyseaux*, Paris; *Historia Animalium Liber III*, Tiguri; *Ornithologiae*, Bononiae [=Bologna].

28. K. Clark, *Landscape Painting*, Charles Scribner's Sons, New York, 1950, pages 26, 27, 33, 106–109.

29. See page 27 of reference cited in note 26.

30. *The Ornithology of Francis Willughby* [etc.], London. English edition published two years after the Latin.

31. See R. M. Mengel. "Audubon." *Dictionary of Scientific Biography*, Vol. 1, pages 329–332, Charles Scribner's Sons, New York, 1970.

32. W. H. Fries. *The Double Elephant Folio*, American Library Assoc., Chicago, 1973.

33. See the MacMillan edition of *The Birds of America* of 1937 (from the Havell plates, reproduction inferior) and the American Heritage edition of 1966 (from the original drawings). All 435 plates have also been reproduced in facsimile at original size by Johnson Reprint Company, 1971–1973. (Sold for $6,900.) A thorough summary of reproductions is given by Fries (as cited in note 32).

34. *A Treasury of Art Masterpieces*, Simon and Schuster, New York, 1939.

35. See C. A. Wood, *Ibis*, 67:594–599, 1925.

36. *Scientific American*, 216:155–158, 1967.

37. Elegantly considered by S. Sitwell, H. Buchanan, and J. Fisher. *Fine Bird Books*, Collins and Van Nostrand, London and New York, 1953.

38. My friend, Gordon Sauer, spent countless hours with the large Gould collections at the University of Kansas, and elsewhere, at this effort.

39. *Traité de Fauconnerie*. Arnz and Co., Leiden and Dusseldorf, 1844–1853.

40. Biography: M. F. Boynton. *Louis Agassiz Fuertes*, Oxford Univ. Press, New York, 1956.

41. Don Eckelberry (*Living Bird*, 2:77, 1963) finds "grave compositional faults" in this picture, suggesting that its background "would require severe cropping" partially to compensate for "areas not structurally tied into [it]." I suspect that this is a *lapsus*; at least, after long consideration, I see no important way of improving on the composition, which has little room for severe cropping.

42. By F. M. Bailey. U. S. Biological Survey, Washington, and New Mexico Department of Game and Fish, Albuquerque, 1928. (And better reproduced in the catalogue of the bird art show that accompanied the 1926 meeting of the [then] Cooper Ornithological Club.)

43. By E. H. Forbush. State of Massachusetts, Boston, 1925–1929.

44. L. A. Fuertes. *Album of* [32] *Abyssinian Birds and Mammals*. Field Mus. Nat. Hist., Chicago, 1930; L. A. Fuertes and W. H. Osgood. *Artist and Naturalist in Ethiopia*, Doubleday, Doran and Company, New York, 1936 (text and 16 plates, somewhat cropped).

45. For many works see F. G. Marcham, *Louis Agassiz Fuertes & the Singular Beauty of Birds*, Harper and Row, New York, Evanston, San Francisco, and London, 1971 (bibliography of appreciations which reproduce other selected works).

46. See J. Fisher. *Thorburn's Birds*, Ebury Press and Michael Joseph, London, 1967.

47. For many fine reproductions see F. P. Jaques. *Francis Lee Jaques*, Doubleday Company, Garden City, New York, 1973.

48. For recent work see his several books published by the University of Oklahoma Press.

49. W. J. Schaldach. *Carl Rungius*, Countryman Press, West Hartford, Vermont, 1945, page 74.

50. There are 50 pictures in W. Kuhnert and R. Lydekker. *Animal Portraiture*, Frederick Warne and Company, London and New York, 1912.

51. W. J. Schaldach. *Carl Rungius*, Countryman Press, West Hartford, Vermont, 1945, page 104.

52. See also D. R. Eckelberry. *Living Bird*, 2:69–82, 1963, in which this author compares Liljefors, Audubon, and Fuertes.

53. B. Liljefors. *Ute i Markerna*, Bonnier, Stockholm, 1912; *Det Vildas Rike* [The Wild Kingdom], Bonnier, Stockholm, 1934; B. Lindwall and L. Liljefors. *Bruno Liljefors*, Rabén and Sjögren, Stockholm, 1960.

54. *Audubon*, 80:70–105, 1979, including page 105 by D. R. Eckelberry.

55. W. J. Schaldach. *Carl Rungius*, Countryman Press, West Hartford, Vermont 1945.

56. For other reproductions see L. E. Render, Provincial Museum and Archives of Alberta, Edmonton, Publ. no. 1, 24 pp. + covers, 1969.

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COMPARATIVE ECOLOGY OF THE MOUNTAIN AND CALIFORNIA QUAIL IN THE CARMEL VALLEY, CALIFORNIA

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The Mountain Quail *(Oreortyx pictus)* is a large secretive bird that inhabits steep mountains and dense vegetation. Because of its peculiar habits the natural history of the species is little known [*17, 27*]. Early western naturalists often noted the difficulty of working with this quail [*3, 8, 21, 22, 46, 47*]. The fact that the bird is locally migratory over much of its range adds to the formidability of studying it. It was not until the publication of a brief account of the bird in 1918 [*15*] that the interesting natural history of the quail became generally available. Significant papers [*41, 43, 50, 53*] followed this work and added to the knowledge of its natural history so that formal questions could be proposed and tested.

The California Quail *(Lophortyx californicus)*, on the other hand, is conspicuous and common and inhabits most plant communities below the zone of Mountain Quail occupancy throughout California and other West Coast areas [*35*]. Thus, it has stimulated a great deal of research on almost all aspects of its biology (reviewed in Leopold [*35*]).

Mountain and California Quail range through all of California's plant communities except the driest deserts and highest spruce-fir, alpine zones. A zone of sympatry occurs annually at the upper limits of the California Quail's range when winter snows drive migratory populations of Mountain Quail from their high mountain homes. In other areas the quail are sympatric all year, yet their ecological relationships in either sympatric situation are unknown. North American Odontophorine quails, however, are regarded as a closely related group [*27*].

In this study I observed and quantified the modes of ecological segregation between the Mountain and California Quail where they are continually sympatric. Additionally, I have tried to elucidate the natural history of the Mountain Quail.

Methods

Study Areas

The primary study areas were located approximately 39 kilometers southwest of the Carmel River mouth on the 809-hectare Hastings Natural History Reservation and adjacent Madrone Canyon on the Palo Escrito Ranch (Figure 1). The elevational gradient over which I worked was 427 to 974 meters. Over 90 percent of my collecting was done in Anastasia Canyon (1.6 km south of Hastings) and on Rana Creek Ranch (3.2 km northwest of Hastings). A limited number of birds were taken from Palo Escrito Ranch, adjacent Bell Ranch, Willow Creek (8 km southeast of Hastings), Piney Creek (6.4 km southeast), and Junipero Serra Peak (16 km southeast). These more distant areas all satisfied the criteria for sympatry (see methods below).

I chose this area because (1) both species are resident year round; (2) both species were initially observed in mixed flocks; (3) habitat diversity is high; and (4) similar collecting localities were available nearby.

Griffin [*11*] adequately reviewed the geology, soils, and climate of the Hastings Reservation. Annual precipitation fluctuated widely from year to year. For example, during the study 53.29 centimeters of rain fell in the wet season of 1973/1974; 68.83 cm in 1974/1975; 26.08 cm in 1975/1976; and 30.2 cm in 1976/1977.

Quail populations are noted for their positive response to breeding when rainfall is high [*35*], so that one can infer from these rainfall data that quail numbers were high at the start of the study and declined dramatically since that time.

Mountain Quail are not migratory here because snowfall is infrequent and seldom lasts for more than a few hours. However, one heavy snowfall on 1 January 1974 broke many chaparral and evergreen tree crowns, thereby creating more quail cover.

The major vegetation zones of the Coast Range are represented in the upper Carmel Valley [*11*] and it was ideal for this study because of the mosaic of vegetation types. Five vegetation zones were defined for this study: Mixed Evergreen Forest, Foothill Woodland, Riparian Woodland, Chaparral, and Grassland (see Griffin [*11*] and White [*60*] for a more complete description of these zones). A sixth category (Ecotone) was defined where two zones integrated. Heavy grazing and extensive firewood cutting occurred in areas outside the reservation.

Habitat Analyses

The study began on 28 November 1973 and continued until 30 May 1977. During this time I spent 413 days or parts thereof in the field, encompassing all seasons of the year. I evaluated habitat association and selection by the quail both qualitatively and quantitatively.

The first, more important criterion in the study of these sympatric populations was that all sampling, with respect to habitat evaluation, observations, and collection of birds for determining food habits and status of reproductive cycles was conducted in known areas of sympatry. That is, any sample representing one species had to have been taken in an area within 500 meters of a known sighting of the other species. In this way I hoped to prevent the bias of collecting from allopatric populations.

Qualitatively, I recorded the plant community for every covey, pair, or single quail that I encountered during the study. The distributions of these habitat associations were then analyzed using the χ^2 distribution testing for the independency of the samples [*59*]. In addition, I wrote extensive field notes on all aspects of the natural history of the quail. These field notes provide an additional source for evaluating behavioral and ecological relationships of the birds.

Perhaps the most significant factor in the success of the project, at least initially, was the use of a highly trained German short-haired pointing dog. The Mountain Quail is secretive, quiet, and shy, and an unskilled observer, unfamiliar with the ways of this bird, might easily overlook a "hidden" covey or bird. These quail often allow a close approach by another animal without sounding alarm calls or trying to "escape." The dog, on the other hand, hunting under close supervision, could at times locate the birds by scent up to 75 meters away. Once the dog pointed, I could recall him and frequently the quail would resume "normal" activities while I observed. California Quail were more conspicuous and the dog was generally not needed to find them.

I used three types of transects for finding birds: fixed, random, and running. Fixed transects were located in all the representative vegetation zones of the Reservation, and I walked them regardless of the presence or absence of quail to sample the habitats more equitably. These transects varied from two to eight miles in length. The dog was used most efficiently on these transects by working canyon bottoms approximately two hours after sunrise to take advantage of downslope winds, and then as the transects led uphill to ridge tops, we began to encounter updraft winds caused by the warming of the earth. The dog was then able to use the ridges more effectively to search for quail below us. This technique frequently increased my search area up to 75 meters beyond my sight, which was often obstructed by dense understory vegetation. This point is important in that a potential bias was partially eliminated because California Quail are more easily seen than Mountain Quail.

Random transects were used when I could not find quail on fixed transects; when I wished to record other behavior; or when I wished to survey a new area for quail. Running transects were employed the last year (June 1976 to May 1977) to test the hypothesis that the California Quail did leave the lowlands and changed habitats in winter as their need for free water decreased. The Mountain Quail were believed to use the same habitats throughout the year. These transects ranged from 3 to 14 miles and were run at a rate of 7 to 8 minutes per mile. They were consistent only in that they always used lowland routes near creeks.

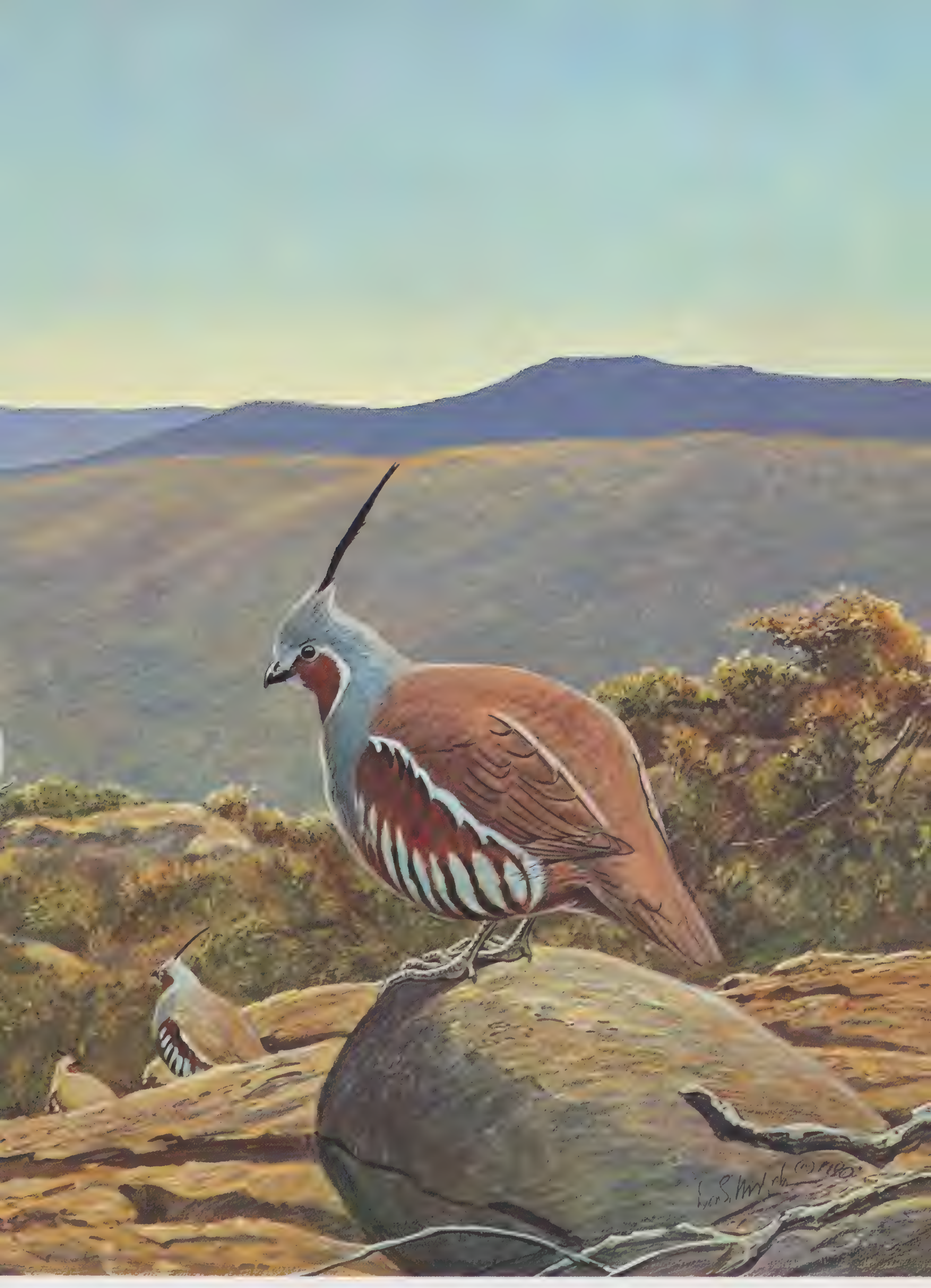

Plate 1. Mountain Quail, *Oreortyx pictus*. Painting by Donald Leo Malick.

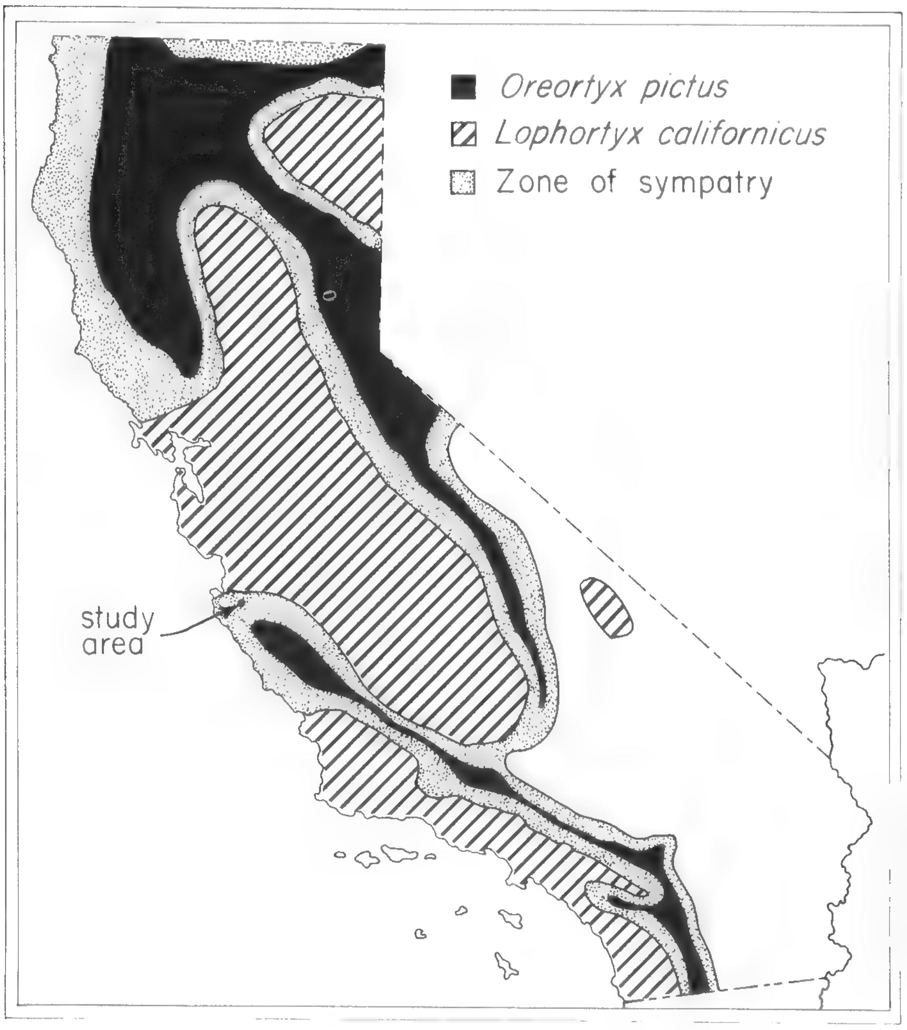

Figure 1. Distribution of Mountain and California Quail in California showing hypothetical zones of sympatry.

I attempted to locate at least 10 coveys or pairs of each species per month between June 1975 and May 1976 using both fixed and random transects. When I sighted a covey, I used the location of the first bird seen as the center point from which to circumscribe a 15-meter diameter circle (0.02 ha). The following information was then recorded: species, date, approximate location, time of day, behavior of the group when first encountered, covey size, brood size, habitat type, the covey's behavior when flushed, distance flushed from me, tree species, shrub species, and 12 other variables. Eleven of the last 12 were measured as continuous variables and were used in the multivariate statistical analysis (see Appendix 1 for description of these variables).

These habitat parameters were first compared for differences (F test). An intra-group correlation matrix was then calculated for all these variables to observe the correlation among the parameters. Few inter-group correlations were significant beyond those which would be expected (i.e., ground cover with shrub cover) so that further analysis seemed justified. These data were then subjected to a stepwise discriminant function analysis, the mathematical objective of which is to weight and linearly combine these parameters in such a manner that the quail data sets are forced to be as statistically distinct as possible [*48*]. A score on the derived discriminant function is then computed for each covey sighting (i.e., each 0.02-ha data set). This function can be considered to be an axis of geometric space; hence the spatial relationships of the two quail's habitat can be graphically observed. Finally, each covey sighting can be classified as to its species membership based on the variables that were used in the analysis. One measure of the adequacy of the discriminant function can then be observed.

Frequencies of occurrence of trees and shrubs were recorded within the sample plots and subjected to Spearman rank-order correlation analysis.

I first analyzed habitats in a classical manner. Although I could show that the habitats used differed in their frequency of use, the analysis of plant species composition in relation to the two birds was misleading. Secondly, I quantified the habitat of each species using variables that I subjectively felt might be important to the quail's habitat selection. These data were then used in a multivariate discriminant function analysis that was able to separate the species on the basis of some physical and vegetational features of the environment. Multivariate techniques have been little used for the evaluation of gallinaceous bird habitats although it seems that this is a logical next step in the evaluation sequence once the descriptive stage has been accomplished (but see Martinka [*40*]).

Food Habitat Analyses

Ninety-six Mountain (45 males, 32 females, and 19 juveniles) and 109 California Quail (48 males, 40 females, 21 juveniles) were collected in all months of the year during 1975 and 1976. All birds were collected under the same criterion for sympatry as that used in habitat analysis (see above). I stored crop material in formalin-filled glass vials if green plant material was present or in envelopes if only seeds were present. I labeled each container by collection number only, so that species identification was made only after a sample was analyzed. Upon analysis, wet samples were oven dried at 100° F to remove excess water and formalin but not to dry the material. Food items were identified to the lowest taxonomic rank that was feasible and efficient; these items were then hand separated by species and measured by volumetric water displacement. Any item displacing less than 0.1 cc^3 volume of water was considered a trace item.

Analyses of data from sympatric populations were performed by determining the species of food item eaten and by the status of the food resource. For example, Spearman rank-order correlation analysis was used to evaluate the relative importance of the 18 most important genera/species of food items. A species diversity index of foods in all resource states [*18*] was then calculated using the Shannon-Wiener formula [*61*]. Using this same data set I quantified one measure of niche breadth with Simpson's index [*58*] and diet overlap as in Pianka [*52*].

Descriptive notes were taken on foraging methods used by the birds and on the contents of the crops in relation to the phenology of the plants that were being eaten. I measured a sample of the depths of individual foraging pits of both species.

Habitat

In the following analysis, I will document how the two species of quail segregate ecologically through habitat separation and physical features of their environment. Food habits and foraging ecology and reproductive cycles also effectively segregate the two quail. The methodology of some analyses used in habitat-selection studies of other gallinaceous birds suggests that a reassessment of their findings is warranted and, moreover, indicates that the multivariate statistical approach should yield more information on species and/or habitat comparisons.

TABLE 1

Habitat Associations among Sympatric Populations of Mountain and California Quail in the Carmel River Valley, California

*Plant community**	*Mountain Quail*	*California Quail*
Mixed evergreen forest	492 (85)†	126 (26.8)
Foothill woodland	7 (1.2)	31 (6.6)
Riparian woodland	5 (0.9)	30 (6.4)
Chaparral	68 (11.7)	32 (6.8)
Grassland	0	184 (39.1)
Ecotone	7 (1.2)	67 (14.3)
Total sample	579 (100)	470 (100)

*After Griffin 1974.
†Sample size; figures in parentheses are percentages.

TABLE 2

Seasonal Use of Habitats by Mountain Quail in the Carmel River Valley, California

*Plant community**	*Season*			
	Summer	*Fall*	*Winter*	*Spring*
Mixed evergreen forest	177 (82)†	92 (88)	52 (87)	171 (86)
Foothill woodland	3 (1)	1 (1)	0	3 (2)
Riparian woodland	3 (1)	1 (1)	0	1 (1)
Chaparral	32 (15)	9 (9)	6 (10)	21 (10)
Grassland	0	0	0	0
Ecotone	2 (1)	1 (1)	2 (3)	2 (1)
Total sample	217 (100)	104 (100)	60 (100)	198 (100)

*After Griffin 1974.
†Sample size; figures in parentheses are percentages.

Macro-habitat

The classification by plant communities of all 1,049 conveys, pairs, or individuals of both species seen during the study (Table 1) shows that the mixed evergreen forest is clearly the primary habitat of the Mountain Quail with the chaparral the second most important. This quail used other plant communities very little. By contrast the California Quail occurred more commonly throughout the various habitats.[1] The designation of the ecotone plant community—that is, where two zones intergrade—indicates that I was unable to clearly designate whether the birds were in one vegetation type or another. Plant communities on the Reservation are often well defined so this problem arose infrequently, but where grazing occurs, the structure of the vegetation sometimes has been altered so that components of each vegetation type occur together. However, these ecotonal areas in the habitat of the

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[1]—Frequency distributions independent in a 2 × 6 contingency table ($\chi^2 = 489.4$; df = 5; $P<.01$).

TABLE 3

Seasonal Use of Habitats by California Quail in the Carmel River Valley, California

*Plant community**	*Season*			
	Summer	*Fall*	*Winter*	*Spring*
Mixed evergreen forest	61 (26)†	28 (35)	6 (18)	31 (26)
Foothill woodland	6 (2)	8 (10)	6 (18)	11 (9)
Riparian woodland	19 (8)	3 (4)	2 (5)	6 (5)
Chaparral	3 (1)	10 (13)	3 (9)	16 (13)
Grassland	110 (47)	18 (23)	11 (32)	45 (38)
Ecotone	38 (16)	12 (15)	6 (18)	11 (9)
Total sample	237 (100)	79 (100)	34 (100)	120 (100)

*After Griffin 1974.
†Sample size; figures in parentheses are percentages.

California Quail mostly represent foothill woodland and mixed evergreen forest or mixed evergreen forest and grassland situations. In these ecotones the shrub understory has been removed by grazing and/or land alteration and trees have been removed due to logging.

It appears that the Mountain Quail uses the same habitats proportionately throughout the year (Table 2). The frequency of use of the mixed evergreen forest and the chapparal were not independent with season.[2] The same treatment of the data set showed that the California Quail used the two habitats with a frequency that was independent of the season (Table 3).[3]

Running transects covered 207 miles in the dry season of 1977 (April–October) with 24 California and 3 Mountain Quail coveys or pairs recorded. I ran 89 miles of lowland transects during the wet season of 1977 (November–March) with four and five coveys or pairs of California and Mountain Quail recorded, respectively. For both species the frequency of use of the lowland habitats was independent of the season.[4]

The occurrence of tree species in sample plots indicated that the relative order of importance of the various species of trees was similar in the habitat of both quail.[5] This result should be expected because the mixed evergreen forest contains all the tree species found in the other plant communities. The same trend can be noted with respect to the occurrence of the important shrub species.[6] The most frequent shrub to be found in the sample plots was poison oak, *Rhus diversiloba*.

Micro-habitat

The physical features of topography, vegetation, and behavioral relationships — for example, distance to cover — showed generally significant differences when compared for each species (Tables 4 and 5). The few measures that are not significantly different represent a critical resource (water) or behavior. The California Quail, for example, uses the mixed evergreen forest or chaparral for escape cover, loafing, and/or roosting. Therefore, they are probably selecting the cover offered by shrubs as one component of these activities. The higher amount of dead material in Mountain Quail habitat is related to the severe snow storm of 1974 that broke many limbs of evergreen trees and shrubs.

The distance of the sightings of both quail from chaparral vegetation was not significant, and possibly may be accounted for by two factors. The first is that patches of chaparral are interspersed throughout the study area so that a random sample of points might yield the same overall "distance to chaparral." Second, it appears that the quail were not using the chaparral vegetation as frequently (Table 1) as Leopold [*35*] indicated that they did. But my results may have been biased to the extent that coveys of California Quail seen feeding in the grasslands may have had their "headquarters" in the chaparral. Thus, they may have been close to it behaviorally if not physically. Alternatively, the forest could have been providing sufficient cover requirements for the birds. The Mountain Quail's primary habitat

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2—2 × 4 test of contingency ($\chi^2 = 3.39$; df = 3; $P>.05$).

3—2 × 4 test of contingency ($\chi^2 = 58.578$; df = 15; $P<.01$).

4—2 × 2 test of contingency ($\chi^2 = 6.3$; df = 1; $P<.05$).

5—Spearman rank-order correlation analysis for tree occurrence in sample plots yielded a significant difference from 0 ($r_s = 0.73$; df = 7; $P<.05$).

6—Spearman rank-order correlation analysis for shrub occurrence in sample plots yielded a significant difference from 0 ($r_s = 0.65$; df = 17; $P<.01$).

generally abutted chaparral. California Quail frequently were found far from chaparral in summer when securing water or when they began using foothill woodland habitats in the winter; consequently, I found them farther from the chaparral (Tables 4 and 5).

In summary, the Mountain Quail live at higher altitudes, on steeper slopes covered with more shrubs, trees, and protective cover than does the California Quail. The California Quail frequents grasslands (herbaceous cover) more extensively and is generally found in more open areas than Mountain Quail.

The discriminant function analyses clearly indicate that it is statistically possible to distinguish the species' habitats on the basis of the parameters that I measured (Figures 2 and 3). When I located mixed species flocks I gave each species identical values for all the variables within the plot, thus nine samples were identical. California Quail must drink daily during hot weather; however, water is often located in the forest environment. In order to drink, the birds must sometimes move into Mountain Quail habitat. On these occasions they might be found feeding while moving to or from water. Sampling the birds at this time would predictably yield values similar to those of Mountain Quail samples since they are using the latter's "typical" habitat.

Perhaps the greatest value of these analyses beyond their power of discrimination and classification is that the relative order of importance of each contributing variable can be assessed in sequential steps of discrimination [*48*]. Thus the most important variable leading to distinction of the quail's habitat can be identified as each new variable is added. For example, initially crown cover was the most important variable, but after five steps, "slope" assumed this position. A statistical picture can be drawn (Figure 4) to illustrate the habitat of the quail based on the above analyses. This figure is different to the "niche-gestalt" diagrams of James [*26*] in that it merely depicts the statistical values of the variables on an accurate scale.

Use of the Habitat by the Quail

The eyes of a good naturalist are frequently sufficient to identify that component of the environment which "appears" to be suitable to maintain a thrifty population of a species [*14, 33, 34*]. My results also argue qualitatively that the Mountain and California Quail are generally using different plant communities (Table 1), but that overlap does occur. I believe this overlap may be related to five factors: (1) Both species require daily drinking water in hot weather [*35, 43, 53*], so that the need for a critical resource necessitates a movement by the species into each other's habitat. (2) Quail escape to the nearest protective cover when disturbed; thus it can easily be seen that measurements of overlap in my vegetation analysis for escape cover would indicate this tendency to escape into dense protective cover regardless of the vegetative community — clearly an adaptive response. (3) Disturbance by predators, such as accipitrine hawks, frequently will separate members of a covey; if one bird escapes into the habitat of the other species then it may associate itself temporarily with a covey of the other kind until it finds or hears its own covey members. The advantage of this association may simply be that there are more eyes searching for predators in a covey. (4) When populations of both species are high, density affects patterns of distribution in such a way that the quail may become closely associated because the habitats are at, or near, saturation. (5) One species may simply move through the other's preferred habitat to areas of its own suitability.

TABLE 4

Physical Characteristics of the Habitat of Mountain and California Quail in the Carmel River Valley, California

*Variable**	*Mountain Quail (N = 164)*	*California Quail (N = 140)*	*Significance†*
	$\bar{x}$	$\bar{x}$	
Altitude	646 m	589 m	27.2
Slope	28.3°	14.3°	101.3
Percentage of ground cover	40.8	28.2	18.1
Percentage of shrub cover	23	19.8	1.3 *ns*
Percentage of dead material	17.8	7.8	22.8
Percentage of crown cover	58.4	21	109.8
Percentage of herbaceous cover	51.2	68.4	29.4
Distance to free water	184 m	176 m	0.2 *ns*
Distance to cover	0.9 m	10 m	29.0
Distance to chaparral	100 m	145 m	9.1
Number of trees	2.9	1.2	51.5
Basal area of trees	.49 m^2	.17 m^2	14.0
Edge	931	1,049	

*See Appendix 1 for an explanation of the variables.
†One Way ANOVA. All significant F-ratios with df = 1, 302; $P < .01$, unless otherwise noted.

The above hypotheses seem realistic and I have recorded field observations documenting all of these ideas. In one area of Madrone Canyon, two major springs flow perennially. One is in the center of distribution of a population of Mountain Quail while the other is in a zone containing mostly California Quail, yet I made observations of both species at these springs or nearby areas only with the drying of temporary springs. It is also common knowledge that quail seek protective cover when disturbed, especially dense cover. All my observations indicate this, so that measurements of escape habitat are predictably similar in the plant communities on the Reservation which are relatively small and form a mosaic of these zones. During the summer and fall of 1975 I recorded seven sightings of single California Quail associating with Mountain Quail coveys. Populations were high that year and I encountered California Quail everywhere in the study area except in the core of the Mountain Quail habitat in Madrone Canyon. However, the population began to decline in 1976 and 1977 with the result that I regularly found California Quail only in a few locations [*18*]. Also I noted no mixed flocks during low populations. Finally, the data suggest (Table 3) that there is a seasonal change in habitat use by California Quail. This is related to the decreased need for water when the winter rains come and because resident accipitrine hawks "learn" to hunt for the quail near the springs and lowland water areas. The quail generally move away from summering areas to feed and/or to avoid predation pressure. Leopold [*33*] pointed out that harassment of quail by hawks may be a factor as important as predation itself because the birds may be unable to feed properly.

The general habitat classification procedures, therefore, are useful in subjectively analyzing the vegetation zones used by the quail. The analysis of the frequency of occurrence of species of shrubs and trees is of less use and in fact may be misleading. The result of the Spearman rank-order correlation analysis for trees is predictable since the mixed evergreen forest has a

TABLE 5

Physical Characteristics of the Foraging Habitat of Mountain and California Quail in Carmel River Valley, California

*Variable**	*Mountain Quail (N = 79)*	*California Quail (N = 81)*	*Significance†*
	$\bar{x}$	$\bar{x}$	
Altitude	661 m	588 m	23.6
Slope	28.6°	13.0°	86.0
Percentage of ground cover	35.8	13.6	56.7
Percentage of shrub cover	17.6	8.2	13.1
Percentage of dead material	18	2.8	39.6
Percentage of crown cover	62.4	14.8	124.6
Percentage of herbaceous cover	58.2	84.4	66.1
Distance to free water	202 m	171 m	1.4 *ns*
Distance to cover	1.5 m	16 m	25.2
Distance to chaparral	106 m	144 m	3.6 *ns*
Number of trees	3.1	0.9	47.4
Basal area of trees	0.56 m^2	0.17 m^2	7.9
Edge	933	1,096	

*See Appendix 1 for an explanation of the variables.

†One Way ANOVA. All significant F-ratios with df= 1, 158; $P < .01$, unless otherwise noted.

greater number of tree species. However, had the analysis included all the tree species (i.e., those occurring less than five times) then the ranks would not have been significantly correlated. Furthermore, the occurrence rankings of shrubs show a significant correlation between plots. One might conclude that, in fact, the species might be using a similar habitat, but less often than other habitats, perhaps due to some different phenomenon such as competitive exclusion [*20, 30*]. One would then be compelled, presumably, to search for another level of ecological segregation in the birds, such as foods or foraging ecology. In fact, many studies on gallinaceous birds have attempted to associate a bird's occurrence with plant species composition either qualitatively or quantitatively [*6, 19, 44, 54*]. This is sometimes possible, as in the association of Sage Grouse *(Centrocercus urophasianus)* with sage brush *(Artemisia tridentata)* [*51*]; but many species exhibit phenotypic plasticity in their habitat selection responses.

Attempts at sophisticated quantification and analysis of habitats in North American galliforms are lacking (review of habitat requirements in Johnsgard [*27*]) and, moreover, no recent published accounts of the Mountain Quail are available. It is evident that Mountain and California Quail habitats can be distinguished on the bases of vegetation structure and topography. Thus, although the quail overlap in habitat and the plant-shrub community seems essentially the same, the Mountain Quail is using a distinctly different component of these habitats. They use areas of high tree crown cover, abundant shrubs, and steep slopes, and are found inside the forest canopy (Tables 4 and 5; Figure 4). The variable for the percentage of dead material is also an indirect measure of the forest-living preference of Mountain Quail.

Carmel Valley Mountain and California Quail are not as dependent upon the chaparral vegetation as has been suggested for these species by others [*35, 41, 44, 53*]. Perhaps this is related to several factors, one of which is the lack of food resources. Most of the local chaparral, for example, contains monotypic stands of the shrub chamise *(Adenostoma fasciculatum)*. Another might be that the relative abundance of chaparral is not as great as that for the other vegetation types. A third might be that most of the water sources are located in mixed evergreen forest and riparian woodland. My observations do not negate those of other workers but merely reflect the plasticity of habitat selection by these quail. Similar quantitative studies in other parts of the range of the Mountain Quail should be most productive.

Habitat Selection

My discussion thus far has considered only the quail's association with particular plant communities. I shall now consider the question of habitat selection and possible key factors in these habitats that motivate the selection. Lack [*30, 31*] formulated the hypothesis that interspecific competition favored the evolution of adaptive mechanisms for habitat selection, whereby birds could detect their most favorable environment.

Food and cover always have been recognized as essential for the reproduction and life of quail. First Baker [*1*] and then Hildén [*23*] considered these factors as essential to a species' survival (ultimate factors). Proximate factors, on the other hand, are difficult to identify [*23*]. I have no data that relate to the functional aspects of ultimate factors in the California Quail, but I believe that I do have such data for the Mountain Quail. Mountain Quail have a strong behavioral avoidance of open ground or grassland. I have recorded obvious excitement on the part of these quail when they are about to cross a modest opening in the forest canopy (15–30 meters) or chaparral [*18*]. Their reactions can be characterized by alarm calls, alert position of the plume (vertical or forward), intention movements (bobbing of the head

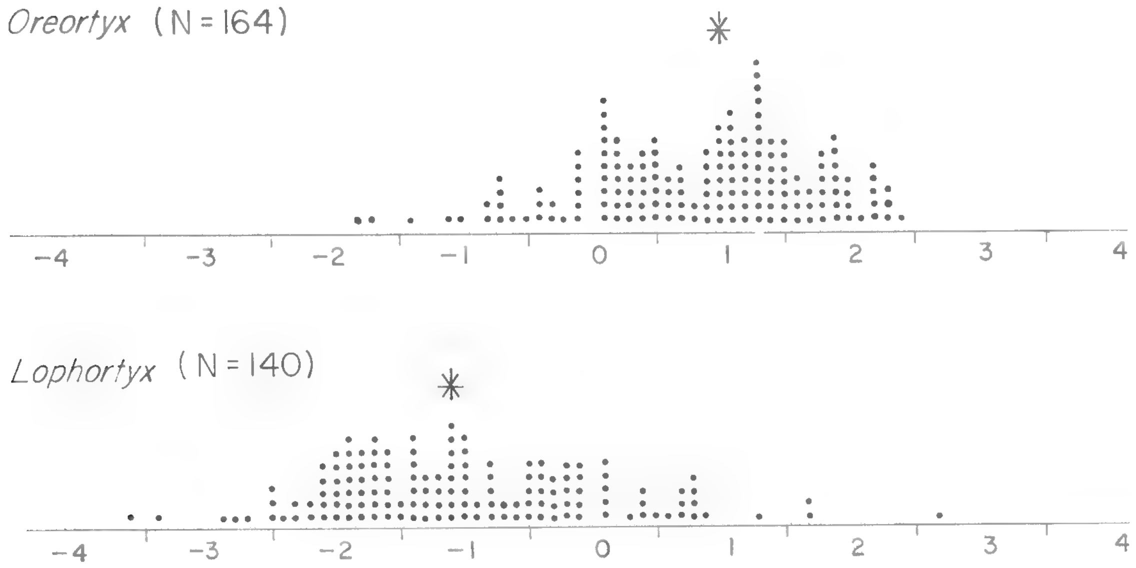

Figure 2. Discriminant scores for all sample habitat plots of Mountain and California Quail. These are the scores on the first discriminant function (linear combination of discriminating habitat variables). The discriminant scores for the sample plots are shown distributed along the discriminant axis to provide an illustrative measure of micro-habitat overlap. Although there is considerable overlap in the distribution of scores of all habitats, the classification procedure documents that the scores (plots) can predict the species quite well. For example, 85 percent of all habitat plots were classified correctly as to group membership ($\chi^2 = 147.8$; $P<.01$; see Nie et al., [*48*] for a discussion of this procedure). The asterisk denotes mean score on the discriminant function.

and/or starting and returning several times before crossing), running across a clearing, and using virtually all available cover in the form of shrubs or dead vegetation when crossing an opening. Every sighting of a Mountain Quail crossing an opening demonstrated at least several of these characteristics. Plume position and running occurred in all cases. Others [*45, 50*] have also noted this preference for dense cover by Mountain Quail.

Predator Avoidance and Habitat Selection

Predator avoidance behavior in the Mountain Quail suggest that these birds would be at a selective disadvantage if they chose habitats in open country. An analysis of these behavioral methods will be presented in detail elsewhere [*18*]. Briefly, these quail most often "freeze" when a predator is sighted; or they seek nearby cover. They then observe the reaction of the predator. If the ground predator attacks, they run first and flush only if capture is imminent. If it is an aerial predator and it attacks, they fly to nearby cover or attempt to go deeper into their present cover patch. I have also witnessed one apparent avoidance behavior for an aerial predator on 6 August 1975, when an entire covey was found by a Sharp-shinned Hawk, *Accipiter striatus*, in a forest opening. Their response was to lie flat against the ground and orient their tails toward the hawk. When the perching hawk flew in a semicircle to gain another visual perspective of the area, all the birds followed the hawk movement by again orienting their tails upward and toward the hawk. I could hardly see the quail even though I was only 15 to 20 feet from them. The hawk evidently did not locate the quail, as it left without pursuit. Perhaps the orientation was one of hiding the contrasting white side flanks of the birds rather than creating a purely disruptive pattern. However, by raising the tail there may be little or no shadow cast by the tail. To my knowledge there has been no recorded anti-predator behavior such as this for a North American galliform. California Quail by contrast frequently freeze when they first perceive a predator, and in my experience they just as often flush. They also seem to flush more frequently than run and at a greater distance than do the Mountain Quail [*18*]. The significance of these behaviors is that a bird which lives in the dense environment of the forest

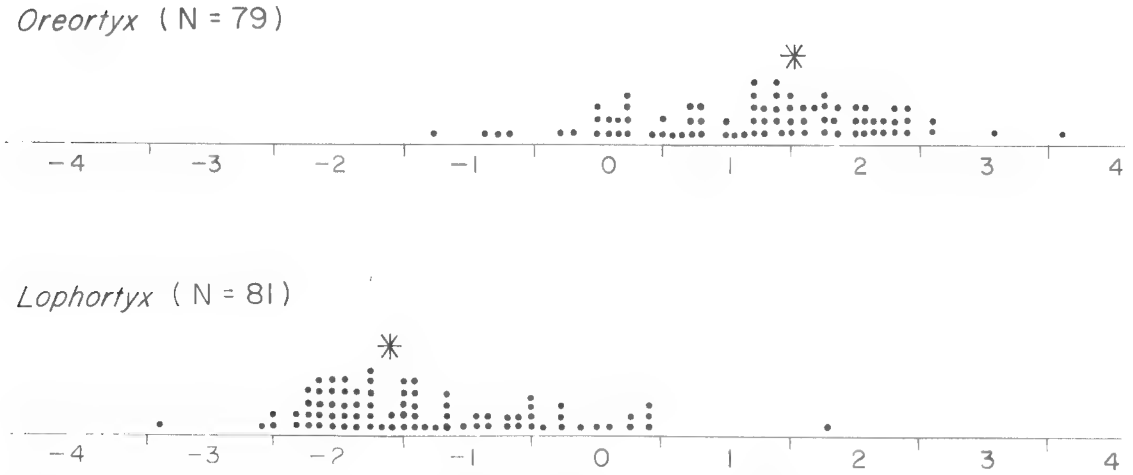

Figure 3. Discriminant scores for foraging habitat plots of Mountain and California Quail. These are the scores on the first discriminant function (linear combination of discriminating habitat variables). Ninety percent of all foraging plots were correctly associated with the species ($\chi^2 = 102.4$; $P<.01$). The asterisk denotes mean score on the discriminant function.

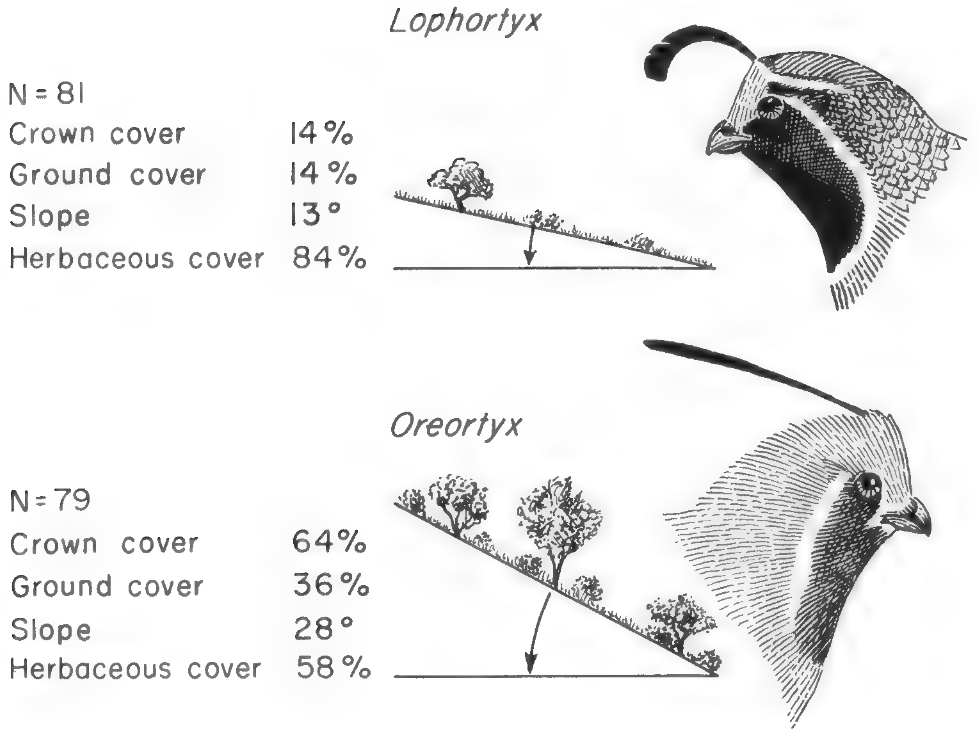

Figure 4. Hypothetical illustration of Mountain and California Quail foraging habitats based on the statistical results of the discriminant analyses.

cannot "afford" to be vocal and conspicuous because, even though they are nearer to cover, so are potential predators. By maintaining a secretive existence and minimizing movement, Mountain Quail are less likely to be detected by predators.

Other Factors and Habitat Selection

The biological significance of water assumes great importance for these birds in that they presumably cannot survive without it [*42, 53*]. It seems that since the young are precocial and need water soon after hatching, those parents selecting a habitat that has water might also be ultimately favored, as the chicks would be more likely to survive. Thus I view ultimate and proximate factors more as a continuum, as individual factors may assume divergent relative positions as different species are considered.

Conclusively indentifying proximate factors is difficult without experimentation [*28*], yet the multivariate analysis provides some insight into these factors by the step-wise extraction method and the relationships to the quantified habitat variables (Tables 4 and 5). Some key factors might be steep slopes and high tree crown cover in my study area for Mountain Quail and herbaceous cover for feeding sites in California Quail (Figure 4). Because numerous naturalists and my own observations have suggested that these factors are important to habitat selection by these birds, the interpretation of the quantified measures of the physical and vegetative characteristics of their environments becomes more meaningful.

Since Mountain Quail are seemingly confined to two specific habitats (Table 1), why do they select only these habitats. Hildén [*23*] discussed the roles of intra- and interspecific competition as factors in spatial bird distribution. The first is related to the density of the population and the second to the presence of species with similar ecological preferences. He noted that many species have narrow habitat preferences on the edge of their range. In fact, Mountain Quail in the Carmel Valley are at the "edge of their range" (Figure 1). They are found in habitat "islands" of mixed evergreen forest on the northern side of the valley, on the steep north facing slopes, although where conditions permit the growth of forest on other aspects, quail also will be found. Competition with the California Quail does not seem to be a factor; Mountain Quail remained in the forest zones after the population of California Quail decreased and disappeared from areas adjacent to Mountain Quail habitat. Mountain Quail maintained relatively more dense populations during this decline than did the California Quail [*18*]. This does not eliminate, of course, the possibility that other species may be competing with Mountain Quail, or that the latter may be keeping California Quail out of its preferred habitat.

One other possible proximate factor exists in the selection for habitats in California Quail. Accipitrine hawks apparently spend a great deal of time pursuing and searching for quail. I saw nine successful captures of quail and numerous other attempts. In summer these hawks hunt in the valley bottoms and near water sources that quail must use. Once the winter rains come, the birds *(Lophortyx)* disperse—usually uphill in my study areas—from the areas of summer concentration as the requirement for free water diminishes. It is also interesting that in the last year of the study (winter 1976/1977) some coveys of *Lophortyx* were seen in their summer haunts throughout the winter and the accipitrine hawk population was apparently low [*18*]. For example, I observed 90, 9, and 2 accipiters during 105 field days in 1975, 134 days in 1976, and 43 days in 1977, respectively. This seasonal movement apparently does not occur in the Mountain Quail, except in spring breeding dispersal, and it could be related, among other things, to their relatively adept predator avoidance behavior in a forest environment.

Food Habits

It is well known from many studies of other birds that closely related species frequently subdivide their food resources by eating different prey, eating prey of different sizes, foraging at different times, and/or foraging in different manners or places [*2, 24, 32, 39, 49, 55*]. The importance of using

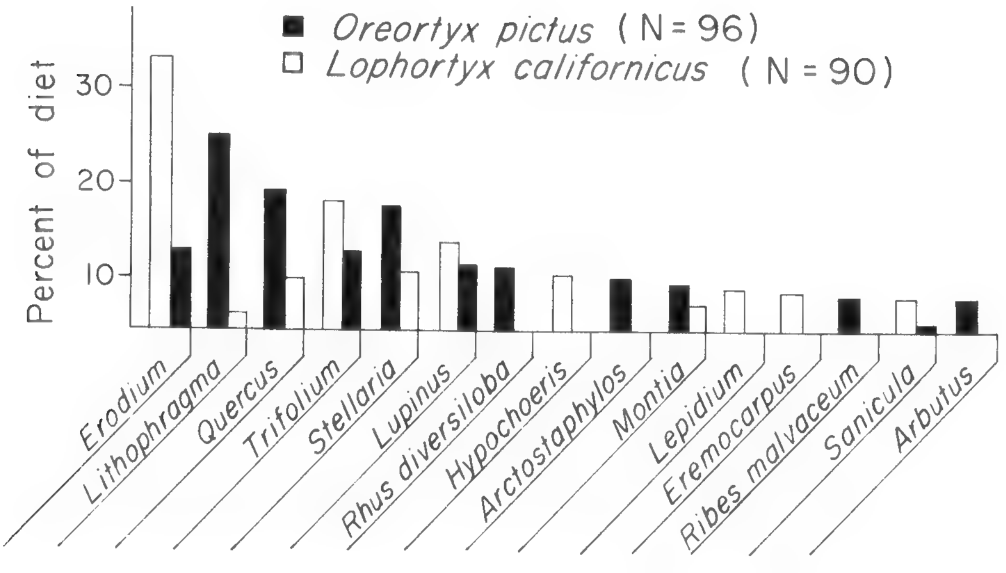

Figure 5. Most important foods eaten by sympatric populations of Mountain and California Quail in the upper Carmel River Valley, California.

separate food resources is clearly a prime consideration in evaluating some aspects of possible competition between the birds. In this analysis, I have tried to relate the differences that I found in the foods eaten by these two quail to the manner in which they procure their food through time and in space.

Both quail exploit a wide variety of food resources—122 food resources by the California Quail and 130 by the Mountain Quail [*18*]. Only a few contribute the majority of the total volume of the diet (Figure 5). This has been shown or predicted for most extensive food habit studies of gallinaceous birds [*16*]. The kind of food and the amount that each kind contributes to the diet can be expected to vary seasonally and geographically [*5*, *18*]. Seventy-nine of the food items identified [*18*] are common to the diets of both quail. It appears that the relative order of importance of the major food items in each quail's diet is different (Figure 5).[7]

Six genera of plants *(Erodium, Trifolium, Lupinus, Stellaria, Hypochoeris, Quercus)* made up over 55 percent of the diet of the California Quail while six genera *(Lithophragma, Quercus, Stellaria, Erodium, Trifolium,* and *Rhus)* made up over 60 percent of the total volume of foods eaten by the Mountain Quail. Thus, annual forbs are the most important foods eaten by *Lophortyx* while perennial plants are more prominent in the diet of *Oreortyx*. It should be pointed out that the high percentage of *Hypochoeris* (smooth cat's ear) eaten by the California Quail can be attributed to sampling error.

Both the relative order of importance of the plant genera eaten by each species, and the type of food harvested (i.e., flowers, fruits, seeds, green vegetation, animal matter, acorns, bulbs, fungi) appear to be quite different (Figures 5 and 6). The consumption of these resources also varies seasonally [*18*].

Diet overlap was calculated to be 0.43. The food resource spectrum of the California Quail was more diverse ($H_s = 3.036$) than was that of the Mountain Quail ($H_s = 2.848$). Similarly, Simpson's [*58*] equation used as an index of niche breadth was higher in the California Quail (14.402) than in the Mountain Quail (11.147).

Foraging Ecology

The Mountain and California Quail differed consistently in their manner of foraging (Figure 7). Mountain Quail commonly dug for bulbs during the dry summer and fall. The depth of a series of diggings of *Oreortyx* ($N = 150$) averaged 4.0 cm. By contrast the scratchings of California Quail averaged only 1.7 cm in depth ($N = 67$). The difference was significant ($t = 13.22$, $P<.01$). I never saw California Quail "dig" when foraging.

On three occasions I recorded Mountain Quail opening acorn hulls for the meat. Miller and Stebbins [*43*] also recorded these birds opening green acorns. On two occasions I found intact acorn halves in the crops of collected birds. I have found only fragments of acorns in the crops of California Quail and I never saw this quail opening an acorn hull. However, California Quail frequent roads where acorns have been smashed by passing vehicles and thus they gather the acorn fragments. Acorns constitute an important item

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[7] —Spearman rank-order correlation analysis of the 18 most important foods in each quail's diet shows that the correlation between their ranks is not significantly different from 0 ($r_s = 0.07$; $df = 29$; $P>.01$).

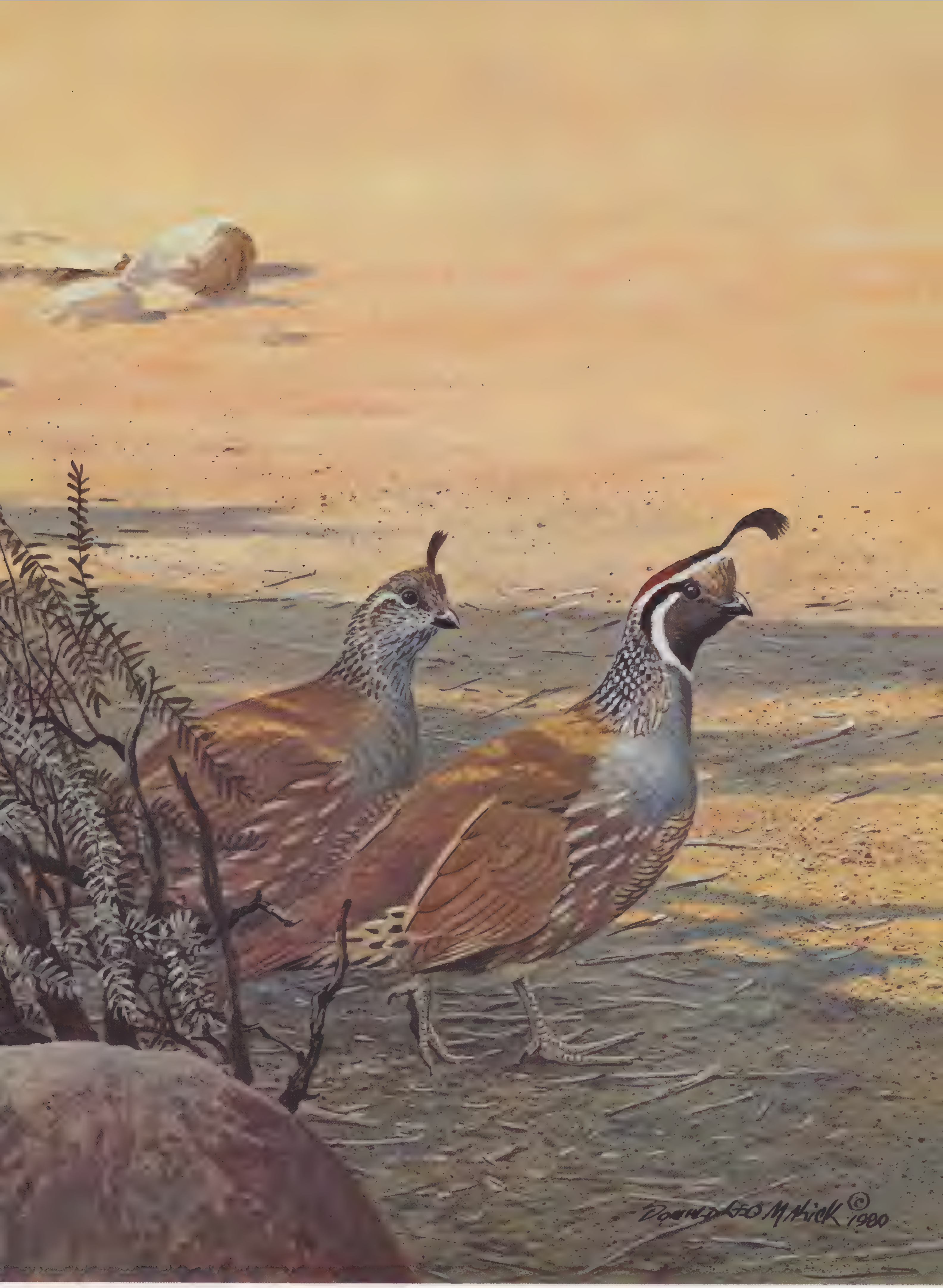
Donald Leo Malick © 1980

Plate 2. California Quail, *Lophortyx californicus*. Painting by Donald Leo Malick.

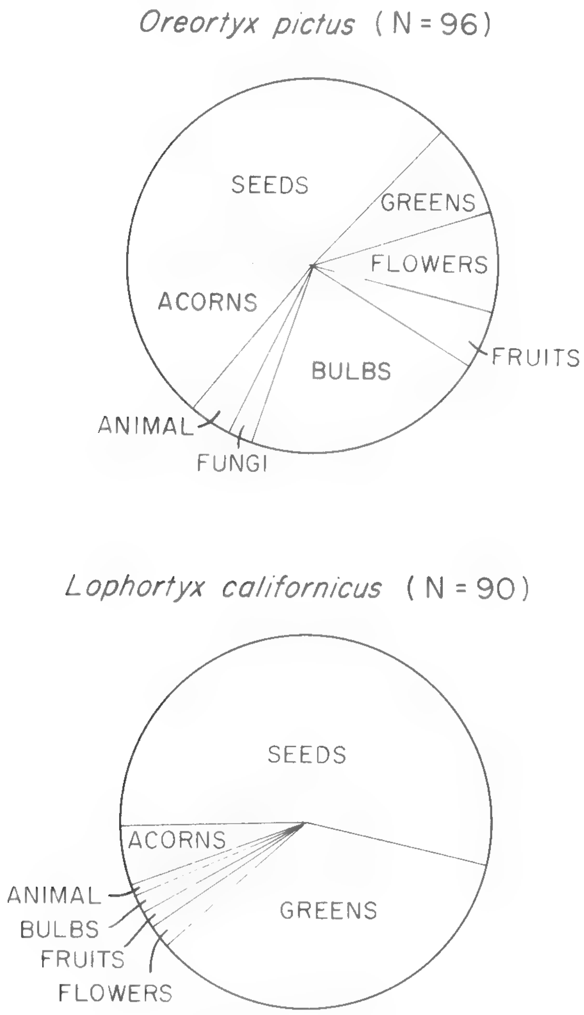

Figure 6. General diet of sympatric populations of Mountain and California Quail in the upper Carmel River Valley, California.

in the diet of *Lophortyx* [*5*], but they must depend on some other mechanical force to open the hulls. However, Linsdale [*37*] suggested these birds may be capable of opening acorn hulls.

On 9 August 1975, I watched a covey of *Oreortyx* forage by jumping for seed heads of a composite (*Madia* sp.) for approximately one hour. The birds jumped about 30 to 45 cm from the ground to secure clusters of the seeds from the stalks. Although this is the only observation that I have made, indirect evidence suggests that it occurs regularly. The winter of 1974/1975 was above average in rainfall. Plant growth was good and *Madia* was abundant. The seed heads were relatively high above the ground (30 to 50 cm), and the shatter of seed capsules did not begin until mid-July.

The crops of quail that I examined showed that Mountain Quail apparently harvested the *Madia* seeds before seed shatter occurred. Furthermore, I found as many seed capsules as seeds of *Madia* in the birds' crops, indicating that they harvested *Madia* before seed capsules shattered. Since the *Madia* plants were tall, the birds either jumped for them, stood on rocks and reached up for the seeds (one observation), or pushed the stalks to the ground (no observations). I favor the first hypothesis since I observed this behavior in the covey of 12 birds on 9 August 1975. California Quail did not begin to harvest *Madia* until the seeds fell and I found only a few *Madia* capsules in their crops. The year 1976 was a poor one for *Madia* and this is reflected in its reduced presence in the crops of collected birds (although the samples were larger). Some Mountain Quail did find and harvest *Madia*

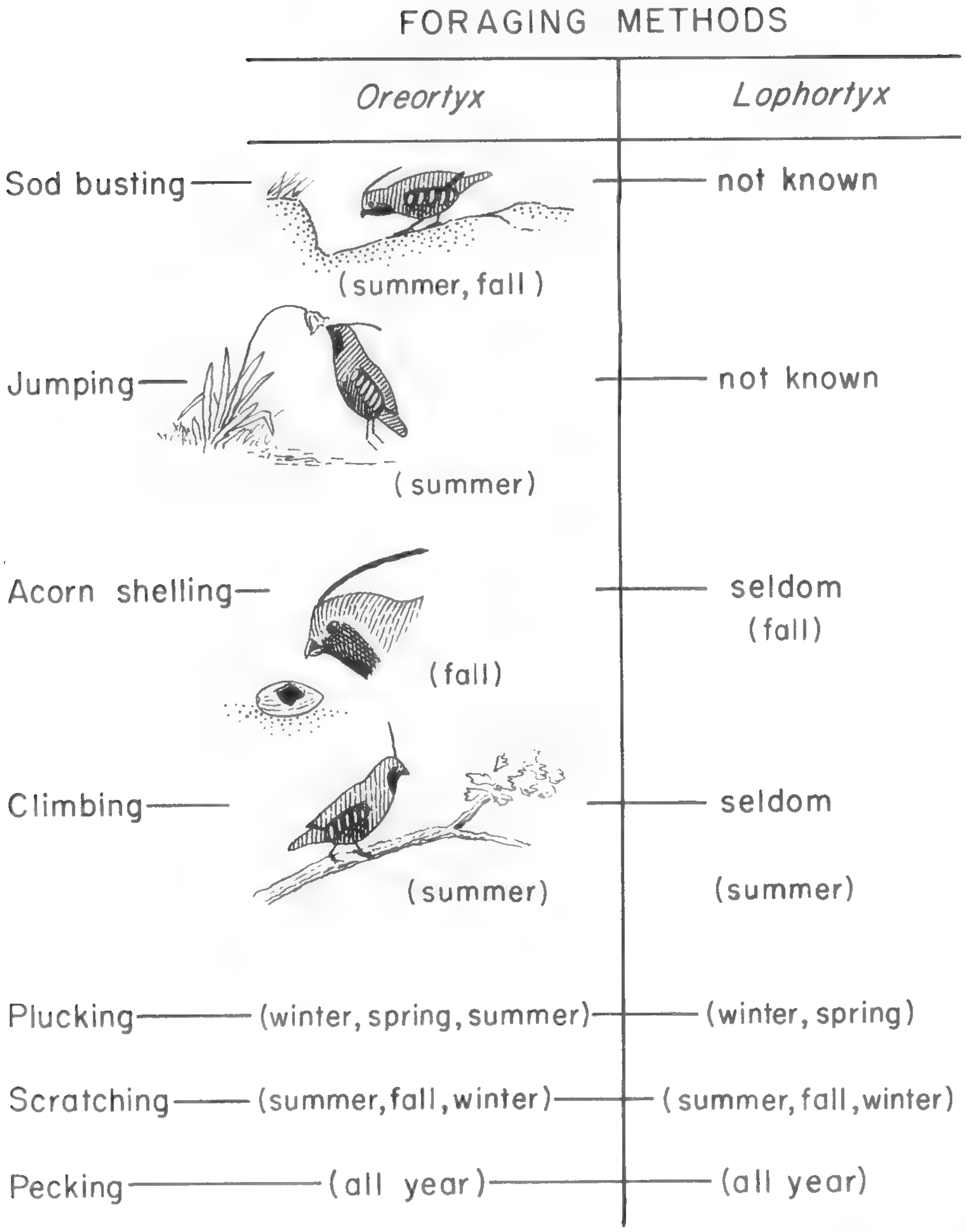
FORAGING METHODS
Oreortyx
Lophortyx
Sod busting
(summer, fall)
not known
Jumping
(summer)
not known
Acorn shelling
(fall)
seldom
(fall)
Climbing
(summer)
seldom
(summer)
Plucking
(winter, spring, summer)
(winter, spring)
Scratching
(summer, fall, winter)
(summer, fall, winter)
Pecking
(all year)
(all year)

Figure 7. Foraging methods used by sympatric populations of Mountain and California Quail in the upper Carmel River Valley, California.

before its seeds shattered in 1976, however. Thus the two quail harvested the same resource but in different stages of ripeness.

Occasionally, I saw Mountain Quail in live oaks gathering the seeds of poison oak *(Rhus diversiloba)*, the vines of which grew among the limbs of the oaks. These quail ate poison oak seeds more than the California Quail [*18*]. Fruit of a currant *(Ribes malvaceum)* and an elderberry *(Sambucus* sp.) occurred in the crops of Mountain Quail about the time the fruits ripened on the bush. Since these fruits also contained the pedicle attachment, Mountain Quail probably plucked fruits from the shrubs. I recorded one large covey (50+) of California Quail harvesting *Sambucus mexicana* berries by climbing for them on 9 August 1975. However, California Quail mostly harvested *Sambucus* berries after the fruit had fallen to the ground in September.

Several methods of foraging are used by both species throughout most of the year (Figure 7). The most important for the California Quail include scratching the litter for seeds and pecking at exposed foods. In winter both species harvest green vegetation by plucking the leaves from growing plants. Mountain Quail, however, continue to use this behavior more in the summer for seed heads and flowers. The decrease in scratching activity in the winter is undoubtedly related to a decrease in seeds as a result of germination.

Division of food resources is one key in the analysis of coexistence of closely related birds [*2, 24, 32, 49*]. These quail seemingly overlap to a considerable degree (.43) although the relative order of importance of the plant genera eaten by the birds is different. It is possible that food competition could be important where both quail use the same habitat; but since they use essentially different habitats, this measure of food overlap is much less of an indication of niche overlap.

Because the Mountain Quail's foraging repertoire is broader than that of the California Quail, it allows them to harvest particular food types (acorns, bulbs), gather foods in different stages of development *(Madia* seeds), and eat seasonal foods (acorns, Madrone flowers, fungi). *Oreortyx* specializes sequentially, using particular food resources as they become available through the year. *Lophortyx*, on the other hand, is a generalist ground-foraging seed eater as are most other North American quail. Only the Mearns Quail *(Cyrtonyx montezumae)* appears to be specialized for digging bulbs [*36*].

This hypothesis for the foraging methods of these birds is consistent with the result of the indices for niche breadth and diversity of food resources. The California Quail has a broader food niche (14.4 vs. 11.1) consistent with greater diversity of foods in its diet (3.036 vs. 2.848) than does the Mountain Quail.

The relationship between food habits and habitat is not merely linear, but is related more to specialized food selection in the Mountain Quail. For example, on 25 January 1975, I collected a male *Oreortyx* and a female *Lophortyx* in the same covey. The birds' crops contained the following foods: *Oreortyx* — *Arctostaphylos* (manzanita) flowers (7.0 cc, 99%), *Rhus diversiloba* (poison oak) seeds (0.1 cc, 1%) and traces of *Trifolium* (clover) leaves, unidentified forb leaves, a *Bromus rigidus* (brome grass) seed, and an ant, *Formicidae; Lophortyx* — *Trifolium* leaves (3.0 cc, 83%), *Erodium* (filaree) leaves (0.5 cc, 14%), *Bromus rigidus* seeds (0.1 cc, 3%), and traces of *Trifolium* seeds, unidentified forb leaves, a grass leaf, and a seed of *Plagiobothrys nothofulvus* (popcorn flower). Although these birds were in the same covey, they had eaten different foods while having access to the same resources.

Both Mountain and California Quail leave their roosts soon after first light and forage until their crops are nearly full. Then, their foraging activity decreases throughout the day as they loaf about cover [*18, 35*]. As evening approaches they again begin to forage intently. Thus, there is little difference in the time of day that the two quail harvest their resources. One minor difference in foraging is that Mountain Quail sometimes show an almost turkey-like behavior as they abruptly cease feeding to move rapidly and undisturbed to another area up to 300 meters away where they begin to forage again. Wild Turkeys *(Meleagris gallapavo)* exhibit a similar behavior except that they may move up to one-half mile before beginning another foraging bout [*29*].

Conclusions and Summary

The foregoing discussion demonstrates that Mountain Quail *(Oreortyx pictus)* and California Quail *(Lophortyx californicus)* effectively partition their resources so that they presumably achieve a state of non-competitive coexistence.

The Mountain Quail selects the forest and chaparral while the California Quail prefers more open woodland, grassland, and chaparral habitats. In central coastal California, a zone of sympatry is the result of a diverse plant community that essentially forms habitat "islands" of mixed evergreen forest for Mountain Quail on the steep, damp portions of canyons that are distributed throughout a "sea" of California Quail habitat. Because these islands are small (less than 300 hectares), the nature of the species' ecological isolation was not obvious from casual observation and thus provoked the question "How do they coexist?"

Lack [*32*] summarized the important ways in which closely related birds could effectively achieve ecological isolation: (1) geographic isolation; (2) selecting different habitats in sympatry; (3) eating different prey or sizes of prey; and (4) foraging in different manners such that the same or different foods could be harvested in different resource states. Mountain and California Quail are geographically isolated for most of the year throughout their range, but during winter they may occur sympatrically as winter snows drive the Mountain Quail from their higher mountain homes. Where they are sympatric for the entire year, at least in the upper Carmel River Valley, they use different plant communities.

During years of high quail populations, California Quail expand their habitat use and zone of occupation so that they overlap with Mountain Quail. Yet the structure of the plant communities that they select is considerably different with respect to the percentage of vegetation and the steepness of the slopes. Mountain Quail, on the other hand, do not appear to expand their range of habitat use in high or low population years. Thus, isolation is effected through habitat selection. Finally, both species may be forced temporarily into similar habitats when a critical resource (water) is necessary for their survival.

Both species eat a wide array of foods yet exploit only a few of these intensively. Their diet overlap is relatively high, but since they are feeding in different habitats the significance of this diet overlap is not as great as it seems at first. Moreover, the Mountain Quail appears to specialize on seasonally available food while the California Quail generally feeds on the seeds and greens of a few annual forbs.

In addition, the Mountain Quail exploits resources unavailable to the California Quail by digging for bulbs, shelling acorns, jumping for seed heads, and climbing for seeds and fruits. It appears that the larger muscle masses and the position and number of sesamoid bones (12 to 13 [*25*]) in the pelvic limb of the Mountain Quail provides the necessary morphological adaptation to allow for a digging movement [*18*]. The California Quail is smaller and only has 2 to 3 sesamoid bones in its pelvic limb [*25*]. Whether the other methods of food harvest are associated with behavioral and/or anatomical adaptations is unknown at this time. Interestingly, California Quail do sometimes harvest bulblets of *Lithophragma* (woodland star) but probably do so by foraging in areas where Mountain Quail have been digging and/or where cattle have walked on steep slopes and their hooves have exposed the bulbs of this plant.

I conclude that, although the general overlap in diet is relatively high (0.43), the manner in which the quail harvest their respective resources through feeding adaptations and methods greatly decreases the importance of the overlap. Also, some overlap may be attributed to a superabundance of some annual plants such as *Erodium*, which grows in most plant communities of the area. Therefore, I believe that, although ecological isolation is primarily effected through habitat selection, foraging behavior and food habits reinforce the primary isolating mechanism.

The levels of ecological segregation that species have attained has been popularly considered to be a result of interspecific competition in their evolutionary past [*7, 30, 31, 32, 38*]. This basic hypothesis is related to the idea of competitive exclusion [*10, 12, 13, 20, 30*] which proposed that no two species with exactly the same ecological requirements can coexist indefinitely.

Gutiérrez and Yang (unpubl. MS) suggested that *Oreortyx* evolved about 11 million years ago (based on their Nei genetic distance data) and that *Lophortyx californicus* diverged from its closest ancestor *L. gambelii* within the last million years. If this last argument is valid, and there is strong evidence that Nei's genetic distance based on allozymes can be used as an adequate predictor of the time of divergence between related taxa [*56*], then I believe that the nature of their present ecological relationships is not easily explained by interspecific competition.

I propose that *Oreortyx* is a much older species than *Lophortyx* and that its current ecology is related to many factors, two of which might be: (1) interspecific competition with other members of its community and/or extinct congeners; and (2) intraspecific competition. When *Oreortyx* was undergoing speciation and early development, it could have interacted only with species other than *Lophortyx californicus*. Whether there were other species of Odontophorine quail sympatric with *Oreortyx* during this time is only speculation, as the quail fossil record is scanty and inconclusive [*4*]. It is clear that there was some adaptive advantage favoring the evolution of *Oreortyx* into a forest, brush dwelling niche since the grassland, open woodland, and savanna habitats were not then populated with California Quail.

The Mountain Quail's behavioral aversion to open country and its anti-predator behavior in dense vegetation suggest that it might have been excluded from the open country habitat by other species of birds, perhaps other quail. Open woodlands and grasslands might have been marginal habitat for *Oreortyx*, as they now are; but it is excluded today by *Lophortyx*—or, *Oreortyx* now excludes *Lophortyx* from the forest. I think this is unlikely, as the Mountain Quail I observed did not extend their range into vacant grassland and woodland habitats during my study. Experimental removal of Mountain Quail from one of their island habitats could provide a further test of their relationships with California Quail. A reverse test occurred with the introduction into Oregon of *Lophortyx*, which spread rapidly, presumably through an unoccupied habitat outside the zone of Mountain Quail occupancy [*9*].

The Mountain Quail's variety of methods for harvesting food may be related to intraspecific competition. Most species of quail in the United States are relatively open dwelling creatures and their thrift depends upon the abundance of a few specific foods [*16, 27*]. I consider only the Mearns Quail and the Mountain Quail adapted to forest and both appear to be specialists to some degree, the former on bulbs of *Oxalis* sp. primarily ([*36*], R. Brown, unpubl. MS), the latter as shown above.

The Mountain Quail does not appear to depend upon the superabundance of annual seeds, probably because these foods are not as prominent in the understory vegetation of the forest and chaparral as they are in open habitat situations. It seems possible, then, that through intraspecific competition for seed resources, natural selection would favor adaptations allowing for the exploitation of a larger variety of food resources. The nature of the Mountain Quail's ecological relationships with other bird species in the forest has not been studied. These interactions might provide fruitful insight into the nature of the present ecology of *Oreortyx*.

I perceive the California Quail as a "boom or bust" species exploiting superabundant seed resources in good years to achieve high population levels and then dispersing into new unpopulated areas. It is opportunistic and a generalist in its approach to habitat selection and feeding. The Mountain Quail appears to be following a different life history pattern. It is larger, probably longer lived, lays fewer eggs per clutch, shows greater parental care, and is more competitive with respect to harvesting food than is the California Quail [*18*].

I also think, however, that studies on the ecology and evolution of *Oreortyx* in areas allopatric to the California Quail should yield a more clear impression of this bird. The strong possibility remains that the life history and complex behavior that I observed may be merely a reflection of its phenotypic plasticity in response to the local environment. Because the forest which the Mountain Quail inhabits at Hastings is floristically depleted and quite possibly depleted of its food resources for quail, the differences that I observed may be related to the use of specialized feeding methods in response to a patchy environment. The size of these small habitat islands may also have influenced their behavioral ecology as they do not appear to be as nomadic as other naturalists have commonly suggested.

It is clear that the evolutionary pathways of these two species have been quite divergent. It is almost fortuitous that their present situation would at first indicate a separation of their ecologies due to competition in the past; but it now seems that the Mountain Quail had evolved long before the California Quail and that their differences are a reflection of their evolutionary ages and not of direct competition.

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APPENDIX 1

Explanation of Habitat Parameters Measured within Sample Plots

Altitude. Elevation above sea level measured with an altimeter.

Slope. Angle of the slope relative to the horizontal, measured with a clinometer.

Aspect. Direction the slope was facing (e.g., west).

Percentage of shrub cover. Line intercept measurement of shrub crowns; two line intercepts were run across the 15-meter circle, one upslope and one across, and their average used.

Percentage of dead material. Line intercept measurement of all fallen oak limbs and dead trees.

Percentage of ground cover. Sum of the percentage of dead and shrub material.

Percentage of crown cover. The vertical coverage of tree crowns over the groundline intercept.

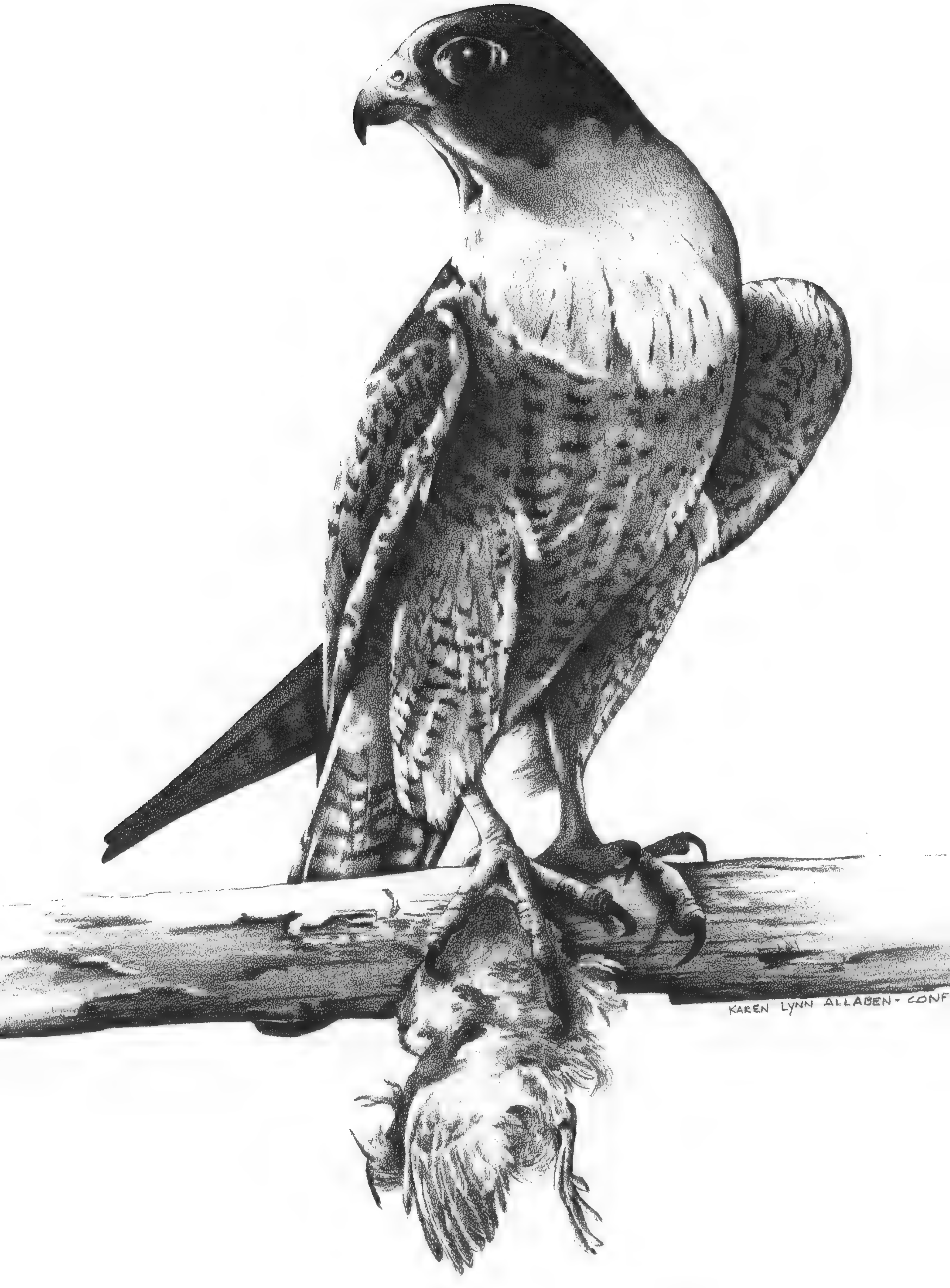
Percentage of herbaceous cover. Line intercept of ground vegetation without respect to the density of vegetation (essentially the line intercept minus ground cover, bare earth patches, water, and rocks).

Distance to the nearest free water source. Distance from the bird to a known permanent spring measured with a range finder or by estimation from a topographic map.

Distance to the nearest chaparral. Measured as above.

Distance to the nearest cover. The distance measured with a range finder from the bird to the nearest suitable hiding place (shrub or brush pile).

Edge. Relationship of the bird to the forest or chaparral boundary or opening in the canopy. A value of 999 indicates that the bird was found at the edge of the opening (opening of 30.5 m or greater in diameter); less than 999 indicates the number of feet inside the forest boundary at which the bird was found, and values greater than 999 indicate that the covey was in an opening (i.e., 1,049 = 50 feet into an opening). The value 999 was chosen as the "edge" value because the farthest observation from a forest edge was approximately 999 feet.


KAREN LYNN ALLABEN-CONF

Peregrine Falcon, *Falco peregrinus*. Drawing by Karen Lynn Allaben-Confer.

LIFE HISTORY OF THE FIVE-STRIPED SPARROW

G. Scott Mills, James R. Silliman,
Kathy D. Groschupf, and Steven M. Speich

The Five-striped Sparrow *(Aimophila quinquestriata)* was known as a breeding bird only from the foothills of the Sierra Madre Occidental of western Mexico, from Jalisco north into northern Sonora, until 1969, when birds with recently fledged young were seen near Patagonia, Arizona [*7*]. Despite evidence of nesting in the United States nearly every year since that time ([*3, 7, 8, 9*]; Bill Harrison, pers. commun.) and the fact that the Five-striped Sparrow is locally common in parts of its range in Mexico [*12*], very little of the life history of this bird is known. Most of the available information is contained in Wolf [*12*] which includes geographic distribution, habitat descriptions, limited data on breeding phenology, and some song analysis. Additional data were provided by Short [*6*] on breeding dates, by Phillips [*5*] on the juvenal plumage, and by Borror [*1*] on the song analysis of one individual. Otherwise, information on this species is limited to brief descriptions in regional works or field guides. Almost no information on its breeding biology has been published and there has been no description of its nest or eggs.

In this paper we report observations of the life history of Five-striped Sparrows in southeastern Arizona from 1974 through 1978. We gathered data primarily on the breeding biology and the status and population dynamics of the species in the United States, but also recorded information on habitats, food and foraging behavior, and winter behavior. We collected most of our data near Patagonia, Arizona, but also include some observations of populations elsewhere in the United States [*2*] and parts of Mexico. Because we conducted the bulk of this study on birds at the periphery of the species' range, some aspects of the life history, especially population dynamics, may deviate significantly from those of populations elsewhere; but we believe much of the information on breeding biology to be representative of the species.

Methods

This study began in August 1974 when Mills and Speich discovered a nest of Five-striped Sparrows near Patagonia. Three more trips were made that year to census the population, band as many birds as possible, and search for more nests. In 1975, Mills and Silliman conducted a thorough study of the breeding biology at Patagonia; from 30 April to 16 September they made over 40 trips to the area. In 1976, Mills and Silliman continued the study and Groschupf began recording vocalizations. Because of a small number of birds and completion of much of the study on breeding biology, the principal objectives of the study in 1977 and 1978 were to record and study vocalizations (results to be published elsewhere). However, we still censused populations and monitored principal nesting activities. We also censused and made casual observations of breeding activities at other locations in the United States, especially Chino Canyon [*2*] in 1977 and 1978. All other populations were in Arizona.

We banded and color-marked most birds for individual recognition every year at Patagonia and in 1977 and 1978 at Chino Canyon. We banded young in the nest or shortly after they fledged. Most adults were netted at nests when feeding older young but some males were netted by decoying them with taped songs. We identified sexes on the basis of song and behavior. Only males sang. We noted no plumage differences between sexes in the field or in specimens examined at the University of Arizona.

Status and Population Dynamics of the United States Populations

From 1974 through 1978, the number of adult Five-striped Sparrows at Patagonia fluctuated between two and ten (Table 1). We recorded more males than females every year except possibly 1978. Pairs attempted to nest every year but the number of young fledged varied considerably (Table 1). We did not census other U.S. populations as carefully and banded only a few birds, but the numbers of individuals at these locations appeared to be relatively constant in 1977 and 1978 except in Chino Canyon where they increased markedly in 1978 (Table 2). Because females are less conspicuous than males and easily overlooked, the numbers of males probably provide the best indications of population changes. Nesting activities were observed at some of these locations in 1977 [*2*] and nests were discovered in 1978.

Because many birds were color-marked, we could determine the return of some individuals. The percentage of banded adults that occurred in successive years at Patagonia varied widely (Table 3). A female banded in 1977 in Chino Canyon was also seen there in 1978. The only young that returned were a male and female in 1975 that fledged in 1974 and one of unknown sex in 1978 that fledged in 1977. One of the two young that returned in 1975 was also seen in 1977 but disappeared before attempting to nest.

Until the winter of 1977–1978, there were no published records of Five-striped Sparrows wintering in the United States; no birds had been observed prior to 25 March or after 29 October in any year. In some years, up to four people conducted thorough searches in early April without success at the site of the Patagonia population. From 1975 through 1977, when we made concerted efforts to determine dates of arrival, Five-striped Sparrows were first seen on 30 April, 28 April, and 2 May, respectively. In 1975 and 1976 we last recorded this species on 16 September and 29 October, respectively. In the winter of 1977–1978, we saw at least two birds at Patagonia in December and January. One was a female that had nested there in 1977 and remained through the summer of 1978. The other was an unbanded bird that had not been seen prior to December. Two birds were also found at two other locations on the same Christmas Bird Count [*10*].

Wolf [*12*] states that there is no evidence that Five-striped Sparrows are migratory. Although the secretive nature of the birds in winter makes their detection difficult, we believe that the careful searches made in early April provide strong evidence that no birds were present at the Patagonia breeding site most winters. The vegetation of southeast Arizona was especially lush during the winter of 1977–1978 due to a very heavy October rainfall. This probably accounted for the winter records that year. We suspect that most birds leave breeding areas most winters, but we do not know where or how far they go.

At Patagonia, the entire population appeared to arrive before June. Only one bird was recorded after 1 July that had not been seen earlier. At some other locations, however, there appeared to be an influx of singing males after mid-July. In 1978, numbers of singing males recorded before

TABLE 1

Populations of Five-striped Sparrows at Patagonia, Arizona from 1974 through 1978

Year	*Males*	*Females*	*Sex unknown*	*Total*	*Young fledged*
1974	4	1	0	5	4
1975	6	4	0	10	15
1976	2	2	0	4	0
1977	1	1	0	2	3
1978	1	1	2	4	0

29 July varied from five to six in Sycamore Canyon (3 trips), three to four in Holden Canyon (4 trips), and one to six in Chino Canyon (7 trips). After July, as many as fifteen males were seen in Sycamore Canyon, eight in Holden, and twelve in Chino. Males that arrived in May and June sang throughout the nesting season, suggesting that there was a real population increase and not just an increase in song.

Habitat

At Patagonia, Five-striped Sparrows were restricted to steep hillsides densely covered with shrubs one to two meters high (Figure 1). This habitat resembles other areas where this species occurs [*2, 12*], but the vegetation at Patagonia is less dense and the area of suitable habitat appears quite small. Dominant plants are the same as in many of the other locations and include kidneywood *(Eysenhardtia polystacha)*, mesquite *(Prosopis* sp.), acacia *(Acacia* sp.), ocotillo *(Fouqueria splendens)*, and chuparosa *(Anisicanthus thurberi)*. As Mills [*2*] suggested earlier, the density of shrubs is probably more important than species composition. Likewise, steep hillsides probably characterize the habitat of Five-striped Sparrows to the extent that they provide the necessary conditions for the correct vegetation structure. Evidence supporting this view is provided by observations of sparrow locations in Sonora, Mexico by J. R. Silliman, and others by S. M. Russell and K. D. Groschupf. Silliman found Five-striped Sparrows to be quite common in an area with little relief

TABLE 2

Populations of Five-Striped Sparrows at Other Locations in the United States in 1977 and 1978

*Location**	*1977*			*1978*		
	Males	*Females*	*Total*	*Males*	*Females*	*Total*
Chino Canyon	2	1	3	12	6	18
Holden Canyon	7	1	8	8	3	11
Sycamore Canyon	12	8	20	15	4	19
Tonto	12	1	13	4†	1†	5†
California Gulch	9	2	11	7	4	11

*All other populations were in Arizona.
†The population at Tonto was not completely censused in 1978.

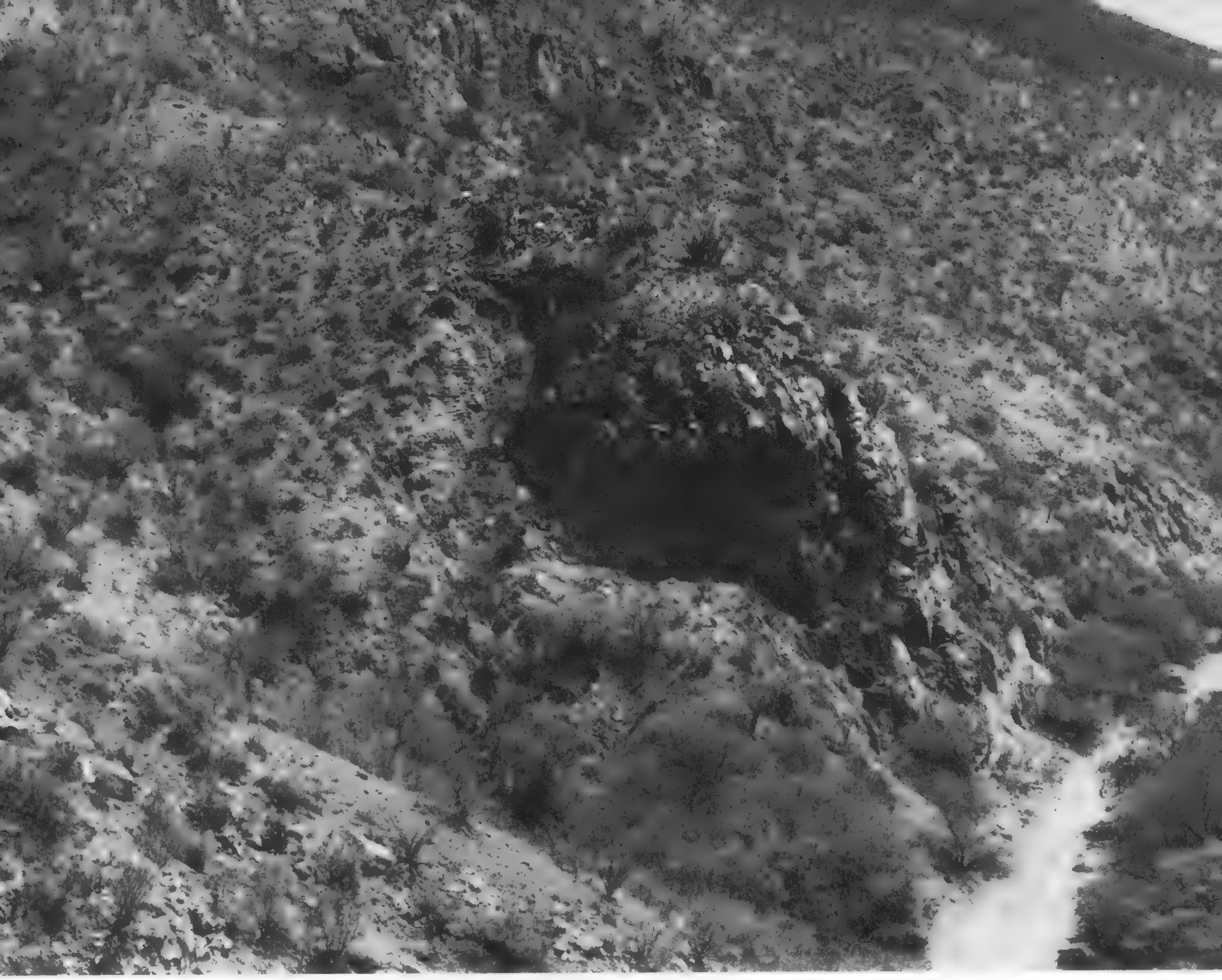


Figure 1. Five-striped Sparrow habitat near Patagonia, Arizona. This species has nested in the canyon in the foreground every year from 1969 to 1979.

approximately 60 kilometers east of Magdalena, Mexico in July 1977. Russell and Groschupf found the species in areas of gently rolling hills approximately 16 km east of Mazacahui, Mexico. Both areas are densely vegetated with shrubs and grasses. Some territories in Chino Canyon in 1978 were also on a nearly flat floodplain in areas of dense vegetation.

Pair Bonds

Five-striped Sparrows form stable monogamous pairs. We do not know if pair formation occurs before or after birds reach breeding sites, but many birds were in pairs when first seen in a given season. Pairs in which both birds were banded remained together throughout the nesting season. In two cases involving pairs with only one member banded, however, pair bonds did not appear to last the entire season. In one, a banded female disappeared in late May or early June after being seen with a male for several weeks; in the other, a banded female appeared to replace an unbanded one in a male's territory in Chino Canyon before nesting began. No pairs were known to remain together for more than one year; but we never recorded both members of a pair in successive years. In 1975 one pair was composed of nest-mates fledged in 1974.

Members of pairs spent much time foraging together before nesting, during nest building, and when incubating females left nests to forage. When pairs reunited after some time of separation, both birds often uttered a distinctive pair-bonding call, probably the warbling song described by Wolf

[*12*]. During foraging bouts, males often flew intermittently to elevated perches and sang before rejoining the female on the ground. Males also accompanied females closely when they were building nests. After leaving the nest, an incubating female often appeared to make an effort to locate the male, who then accompanied her as she foraged. Males usually followed females back to the vicinity of the nest, where they would sing before moving to another part of the territory.

We recorded an apparent solicitation display by a female on 1 July 1978. While a female gathered nest material on the ground, she assumed a posture with bill pointed up, tail down, and feathers erected. While maintaining this posture, she rapidly vibrated her wings, producing an audible sound, and made a series of high piping notes. As her mate approached, she lifted her tail and turned away from him, and copulation occurred. The entire sequence was repeated in a tree a short time later. Copulation was also seen on 15 August 1975, but no displays were noted.

Territoriality

Five-striped Sparrows maintain territories in which mating, nesting, and feeding occur (Type A of Nice [*4*]). Males sang frequently on territory from June to September. A marked reduction in song appeared to occur after the last nesting attempt by the female had started. Males usually sang from elevated perches throughout the territory, using some perches more frequently than others. Singing also occurred frequently, but at a reduced rate, while males foraged on the ground or in shrubs. During April and May, when we usually first saw birds at Patagonia, males sang infrequently and softly; but general territorial sites appeared to be established at that time. Marked birds generally remained throughout the summer in areas where we first recorded them. No more than two birds, presumably male and female, were seen together for any length of time in April and May. Territorial boundaries appeared to break down after fledging of the last brood. Males seldom sang and families often wandered unchallenged into adjacent territories.

Most territories located in the United States were on steep hillsides and included, or bordered, a wash. No territory was above another on a hillside. Because suitable habitat usually occurred only on one side of a wash, a

TABLE 3

Percentages of Banded Adult and Fledgling Five-striped Sparrows that Returned to Patagonia in Subsequent Years

Year	*Percentage of adult males that returned*	*Percentage of adult females that returned*	*Percentage of fledglings that returned*
1975	100 (3)*	0 (1)	67 (3)
1976	0 (4)	33 (3)	0 (15)
1977	0 (1)	— (0)	— (0)
1978	0 (1)	100 (1)	33 (3)
Total	33 (9)	40 (5)	14 (21)

*Numbers of banded birds present in previous years are in parentheses.

territory usually bordered no more than two others. Estimated size of territories at Patagonia ranged from .6 to 2.6 hectares, but activities were usually concentrated in a smaller area near an active nest. This area of concentration changed with nest location. Territory size appeared to be affected by habitat quality; larger territories often contained areas with little shrub cover that, except for occasional foraging, were avoided by Five-striped Sparrows. Territories on the edges of "colonies" were usually in areas where vegetation was less dense.

Territories nearly always bordered obvious topographic features, usually ridges. Slight overlap between territories often occurred, but neighboring males, when present at a joint boundary, behaved as if a fixed line separated them. Boundaries sometimes shifted during a season when another nesting attempt was initiated at a new location within the territory. Most shifts involved boundaries that did not border other territories and thus caused no conflicts. Lengthy agonistic interactions occurred, however, when one male reclaimed much of the territory usurped by an adjacent unmated male. The largest shift in territorial boundaries was made by the same unmated male, who was seen with a female on several occasions in May in an area of about 1.5 ha approximately .7 km from the above pair. The female disappeared sometime in late May or early June and the male began extending his territory toward the pair. For a brief period he ranged over an area of approximately 7.0 ha, but then confined his activities to an area of about 1.0 ha adjacent to the pair.

Some males occupied approximately the same areas in successive years but others shifted their territories to new areas. In a particular canyon, one male held a territory for two consecutive years. At least two other males, one of them unmarked, held the canyon territory for three years. All three females that returned in successive years occupied essentially the same areas both years. Territory size did not appear to depend on population size.

Singing appeared to advertise territories; but during interactions between males at territory boundaries or during territorial intrusions, no singing occurred. At the beginning of an interaction, both males usually chattered; if the encounter was lengthy (greater than two minutes), they often became silent. What appeared to be the highest intensity chatter was very similar to, if not identical with, the "pair bond" call. During these interactions males assumed a posture very similar to the female's solicitation display (see Figure 2). The body stiffened, the wings drooped, and the body feathers, especially those on the rump and flanks, were erected. The tail was often cocked at approximately a 45-degree angle. The head was either extended straight out or at an upward angle, showing the striking markings of the throat to the opposing bird. Both sexes assumed this posture, but females did so only when an intruding bird entered the territory. Aggressive displays by Rufous-crowned Sparrows *(Aimophila ruficeps)* that we saw during this study were very similar to those described above.

At territory boundaries and, in some cases, within territories, both of the males involved in an interaction assumed the posture described above. On two occasions, birds (once a male and once a bird of unknown sex) intruded into territories, foraged on the ground, and appeared to ignore the resident male, which closely followed the intruder from the vegetation and chattered and displayed. Displays at territorial boundaries usually ended with both birds slowly drifting apart, but in the case of the territory overlap described earlier, prolonged chases occurred. On one occasion, the mated male chased

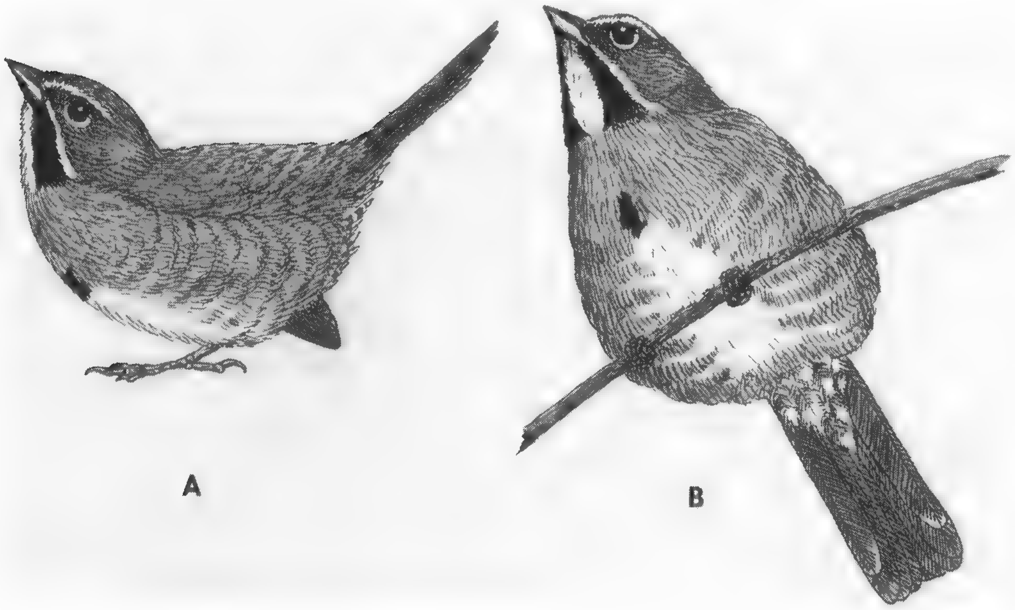


Figure 2. Territorial displays of Five-striped Sparrows. Position A was assumed when both birds were on the ground. Position B was assumed when one bird (shown here) was above the other.

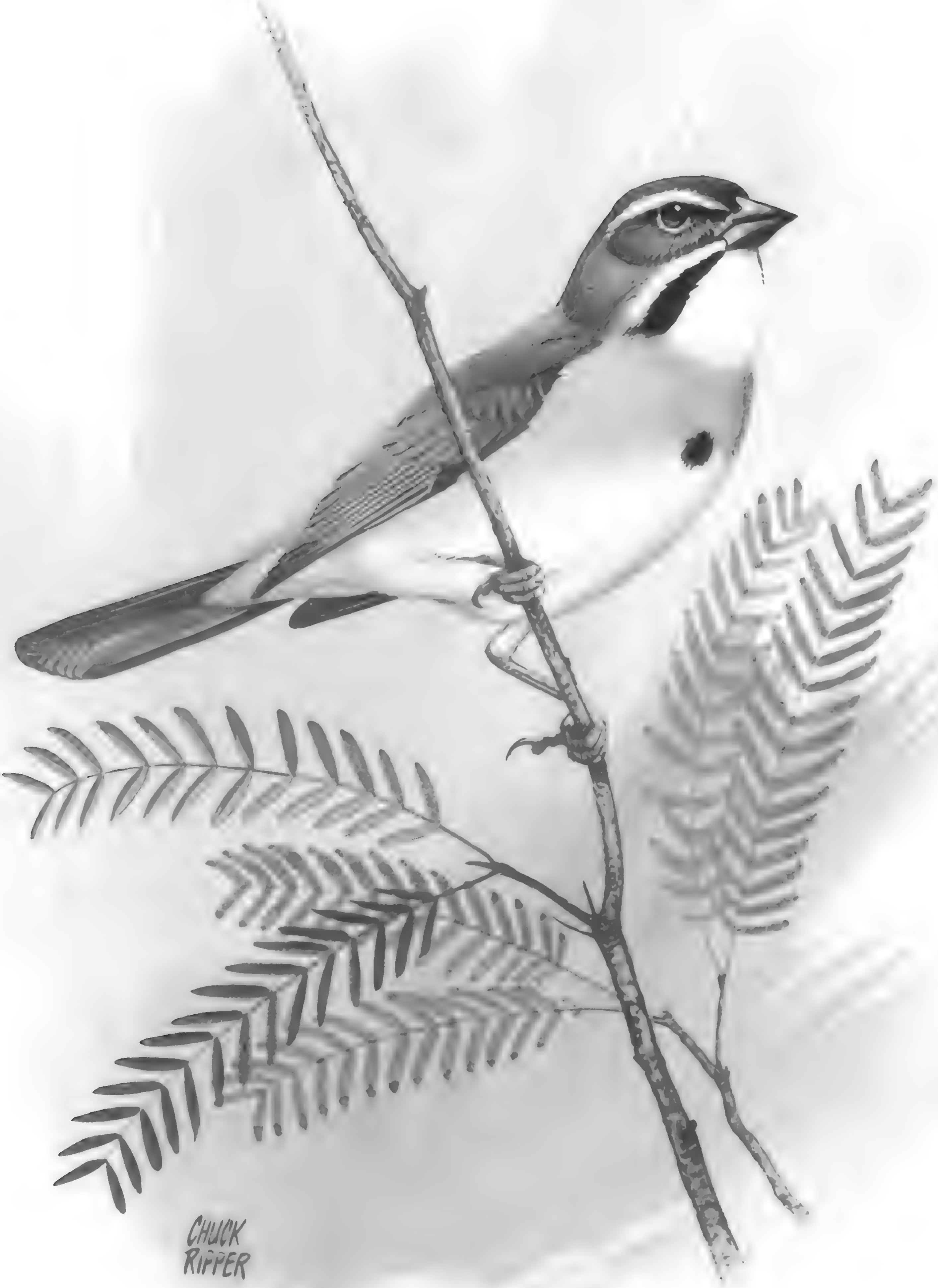
the unmated bird in flight at altitudes from two to ten meters intermittently for over 30 minutes. Chases lasted as long as one minute. Both birds were silent during these chases. When the chased bird landed, the aggressor usually landed nearby, chattered, and hopped toward the intruder.

We recorded the reactions of territorial birds to taped songs. Responses, in order of increasing intensity, included: no response, singing, movement toward the tape with or without singing, and movement toward the tape with chatter and display. Intensity of response was inconsistent but appeared to be influenced by time of year, location of the tape broadcast within the territory, and nesting status of the bird. Some birds appeared to habituate to taped songs.

Five-striped Sparrows also acted aggressively toward some other species and appeared to defend territories against Rufous-crowned Sparrows and Black-throated Sparrows *(Amphispiza bilineata)*. In most interactions between Five-striped and Rufous-crowned Sparrows, which we noted most frequently, the former were dominant. Before and after they maintained territories, Five-striped Sparrows tolerated Rufous-crowned Sparrows and the two species often fed near one another and even appeared to form loose flocks. Rufous-crowned sparrows commonly sang within territories of Five-striped Sparrows in May and June; but in July and August the former moved higher on the hillsides and were rarely heard in territories of the other. Five-striped Sparrows also chased Rock Wrens *(Salpinctes obsoletus)*, House Finches *(Carpodacus mexicanus)*, and Varied Buntings *(Passerina versicolor)*, and displayed to Wied's Crested Flycatchers *(Myiarchus tyrannulus)*. Five-striped Sparrows were chased by Brown Towhees *(Pipilo fuscus)*, Bewick's Wrens *(Thryomanes bewickii)*, Varied Buntings, and Phainopeplas *(Phainopepla nitens)*.

Nesting Phenology

Of nine pairs of Five-striped Sparrows at Patagonia, six nested twice in a season, two nested three times, and one nested once. The number of nests built depended somewhat on nesting success but one pair successfully


CHUCK RIPPER

Five-striped Sparrow, *Aimophila quinquestriata*. Drawing by Chuck Ripper.

fledged young from three nests in one season. Dates of the first egg of the season ranged from 3 or 4 June to 20 July. Dates of the first egg in the last nest ranged from 7 or 8 July to 20 August. Of 26 nests found in Arizona where first-egg dates were known or could be calculated, four were in June, 16 in July, and six in August. A complete nesting cycle, including nest building, lasted 26 to 30 days. Young fledged as late as 8 September and would have fledged on 11 or 12 September from one nest had it been successful. Females laid the first egg of a subsequent nest five to seven days after young had fledged from the first.

Nest Description and Location

Only females constructed nests. Completion of a nest took three to five days. We saw nest building only in early morning before 08:00.

Nests of Five-striped Sparrows are deep cups constructed of grass stems and blades and are placed in vegetation for support. Nests are lined with fine grass, and 14 of 20 nests examined were also lined with horsehair (8 nests) and/or Javelina *(Tayassu tayassu)* hair (8 nests). Nests varied considerably in bulk. Measurements of 20 nests were as follows: outside diameter, 79 to 120 mm ($\bar{x} = 102$); inside diameter, 51 to 73 mm ($\bar{x} = 67$); outside depth, 64 to 140 mm ($\bar{x} = 91$); and inside depth, 47 to 90 mm ($\bar{x} = 63$). Nest size did not appear to be affected by the type of plant in which it was placed or the time of year it was built. Most measurements were made after the young fledged or the nest was abandoned, but before we collected the nest (21 nests are in the University of Arizona collection).

Nests were built in a wide variety of plants. Of 26 nests found in Arizona, six were built in grass clumps (those identified were *Digitaria californicum)*, two in the bases of ocotillo, and 18 in shrubs. Of those built in shrubs, four were in *Condalia* sp., four in *Aplopappus laricifolius*, three in *Celtis* sp., two in *Dodonea viscosa*, and one each in *Aloysia wrightii, Anisicanthus thurberi, Atriplex* sp., *Baccharis* sp., and *Tecoma stans*. The single nest found in 1974 and four of eight nests found at Patagonia in 1975 were in grass clumps, but all eight found there in 1976 through 1978 were in shrubs. Individual females showed no preference for any one location; one female built successive nests in a grass clump, an ocotillo base, and a shrub. Heights of nests (rim to ground) varied from 19 to 150 cm but only 3 of 21 were above 1 meter. Most nests were inconspicuously located in heavy foliage of the nest plant and sometimes vines *(Nissolia schottii* and *Cocculus diversifolius)*. Some nests were in shrubs overshadowed by a large plant, usually a mesquite or acacia. Two nests were built in the relatively open understory of hackberry-mesquite thickets.

Females placed nests in many locations within a territory, often on the periphery. The success or failure of a nest appeared to influence the location of a subsequent nest. A female built her subsequent nest near the previous one if her young had successfully fledged from it ($\bar{x} = 23$ m, $N = 4$), but at a considerably greater distance from the previous nest if it had failed ($\bar{x} = 131$ m, $N = 5$). Differences in distances between successful and unsuccessful nests were significant ($t = 4.7$, $p<.01$).

Eggs and Incubation

Eggs of Five-striped Sparrows are dull white and unmarked (Figure 3), much like those of other *Aimophila* [*12*]. Mean length of nine eggs that failed

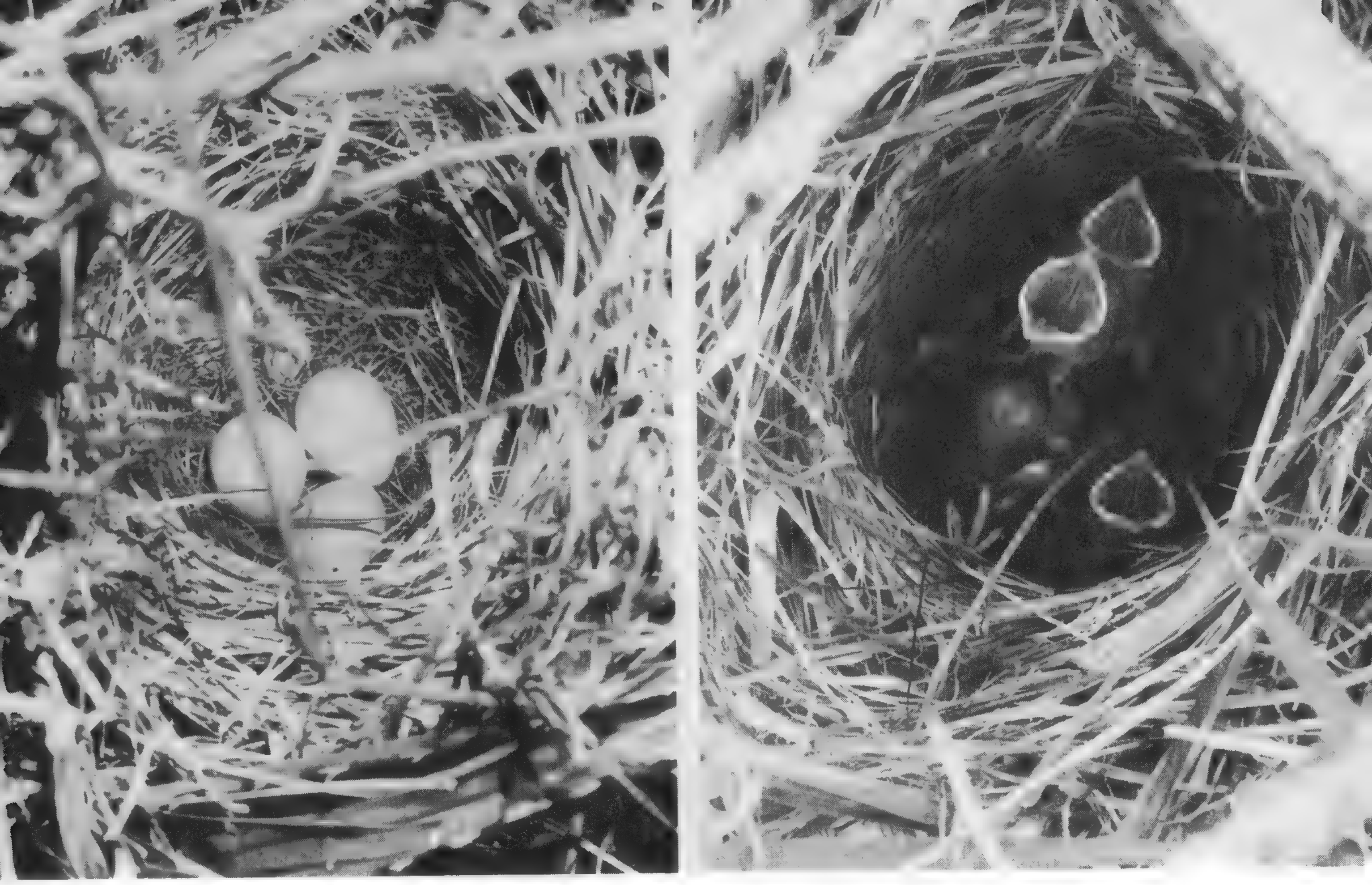


Figure 3. Nests with eggs and four-day-old young of Five-striped Sparrows.

to hatch was 19.8 mm (range, 18.8 to 20.3), mean width 15.5 mm (range, 15.0 to 16.0). Six of seven nests in which the first egg was laid before 14 July contained clutches of three eggs, whereas six of eight nests in which the first egg appeared after 14 July contained clutches of four eggs. These were nests not parasitized by cowbirds. This pattern differs from that of most birds, in which the year's first clutch is usually the largest [*11*], and is probably an adaptation to an increased food supply resulting from summer rains that usually begin in late June or early July. Four nests containing clutches of two eggs also held an egg of a Brown-headed Cowbird *(Molothrus ater)*.

Females laid one egg each day. Incubation began with the second egg of a three-egg clutch and apparently with the third egg of a four-egg clutch. The female alone incubated the eggs for twelve to thirteen days. In three-egg clutches one egg usually hatched one day later than the other two. Of thirty-three eggs in eleven nests that were not taken by predators, twelve eggs in six nests failed to hatch. In four of these nests unhatched eggs remained after the young had fledged. Six of the eggs that failed to hatch were laid by one female in two nests in one year, although eggs laid by her the previous year had been fertile. None of these eggs showed any sign of embryonic development,whereas at least one of the other eggs that failed to hatch contained a large embryo. This female incubated a clutch of four infertile eggs for seven days after they should have hatched, at which time we removed them.

Nestlings

Newly hatched Five-striped Sparrows are naked except for dark gray down on the head and back. Eyes are closed and the young make no audible sounds. By the age of four days the eyes are open and wing and body feathers have appeared but are short and entirely sheathed, or nearly so. Well developed yellow rictal flanges are present and the mouth linings are bright red. A high thin peeping sound, first audible at the age of three days, is made when an adult comes to the nest or if the nest is jarred. By the age of six to seven days, the remiges are breaking the sheaths and the rectrices are short and sheathed. Body feathers have broken the sheaths and the bird appears fluffy, but some areas between feather tracts, notably the belly and sides of the rump, are still naked. At the time of fledging, the body is fully covered with dark grayish-brown feathers with streaks of dull white below (Figure 4). Wing feathers are sheathed only at the bases and the birds are capable of short flights immediately after fledging. The tail is still very short but the tips of the feathers are unsheathed. Fledging usually occurs at an age of nine or ten days. Fledging may occur when the young are only eight days old if the nest is disturbed. In this case, all young leave the nest and do not return. If young eight to nine days old were handled gently in the absence of adults, they could be removed and replaced and the nest would not be abandoned. Nest abandonment is accompanied by rapid "ticking" by the young and apparently is triggered by adult alarm calls; it decreases when an adult appears with food. All young that fledged early, and were looked for later, survived for at least one week.

Nestlings were fed by both adults. Females appeared to do most of the feeding when the young were newly hatched; but males appeared to increase their feeding role so that when young were four to five days old the sexes shared the task equally and alternated their visits to the nest. When air temperatures were high, females often brooded young. When brooding, females stood on the sides of the nest and frequently raised and slowly lowered the feathers of the rump, a behavior which we assume has some thermo-regulatory function. At one nest containing four- to five-day-old young, the female brooded the young four to five minutes after each feeding.

Fledglings

Young Five-striped Sparrows are cared for by both adults for the first four or five days after fledging. If the female renests, once she is incubating the subsequent clutch, the male takes full charge of the young. We saw one female building a new nest and feeding her young on the same day. Once the female begins incubating, she is aggressive toward young from her previous brood and drives them from the vicinity of the new nest. Both adults share in the feeding of fledglings from the last nest of the year. In one case, involving three juveniles, the female appeared to do the majority of the feeding; in another case, involving four young, the male fed two young and the female the other two. In the latter case, we rarely saw the two groups of young together. Adults fed their young up to 18 days after fledging, but the juveniles were also feeding on their own at this age. We saw young following adults and begging for food as late as 30 days after fledging, but we did not see adults feeding juveniles at this age. One group of juveniles remained with their parents for at least 42 days after fledging but fed entirely on their own when last seen.

The timing of plumage changes from fledgling to adult varied to some degree, but followed a predictable pattern. The streaks on the underparts gradually cleared so that by the 15th to 18th day after fledging, the belly was an unstreaked light yellow and the sides and chest brownish-gray. By this age the tail was approximately three-fourths the adult length. Rictal flanges were still conspicuous. By the 20th day, the young resembled drab adults; plumage was brownish-gray rather than gray; malar stripes were dark brownish-gray instead of black; and the white throat stripes were gray, not white. The belly was still light yellow rather than white. The white supercilliaries were somewhat developed on one bird 15 days after it had fledged, but they were not conspicuous on most others until about 40 days after fledging. The black chest spot was noticeable at an age of about 22 to 24 days after fledging. Forty days after fledging, the young closely resembled adults except that the white head markings were less distinct and many retained the yellowish belly.

Predation and Parasitism

We recorded no predation on adult Five-striped Sparrows and only one of twenty adults at Patagonia disappeared before, or during, the nesting season. However, this species showed alarm reactions to a number of potential predators and were seen scolding or mobbing Elf Owls *(Micrathene whitneyi)*, Roadrunners *(Geococcyx californianus)*, gray foxes *(Urocyon cinereoargentatus)*, rock squirrels *(Citellus variagatus)*, and Sonoran whipsnakes *(Masticophus bilineatus)*. Other potential nest predators seen in the area included gopher snakes *(Pituophis melanoleucus)* and Mexican Jays

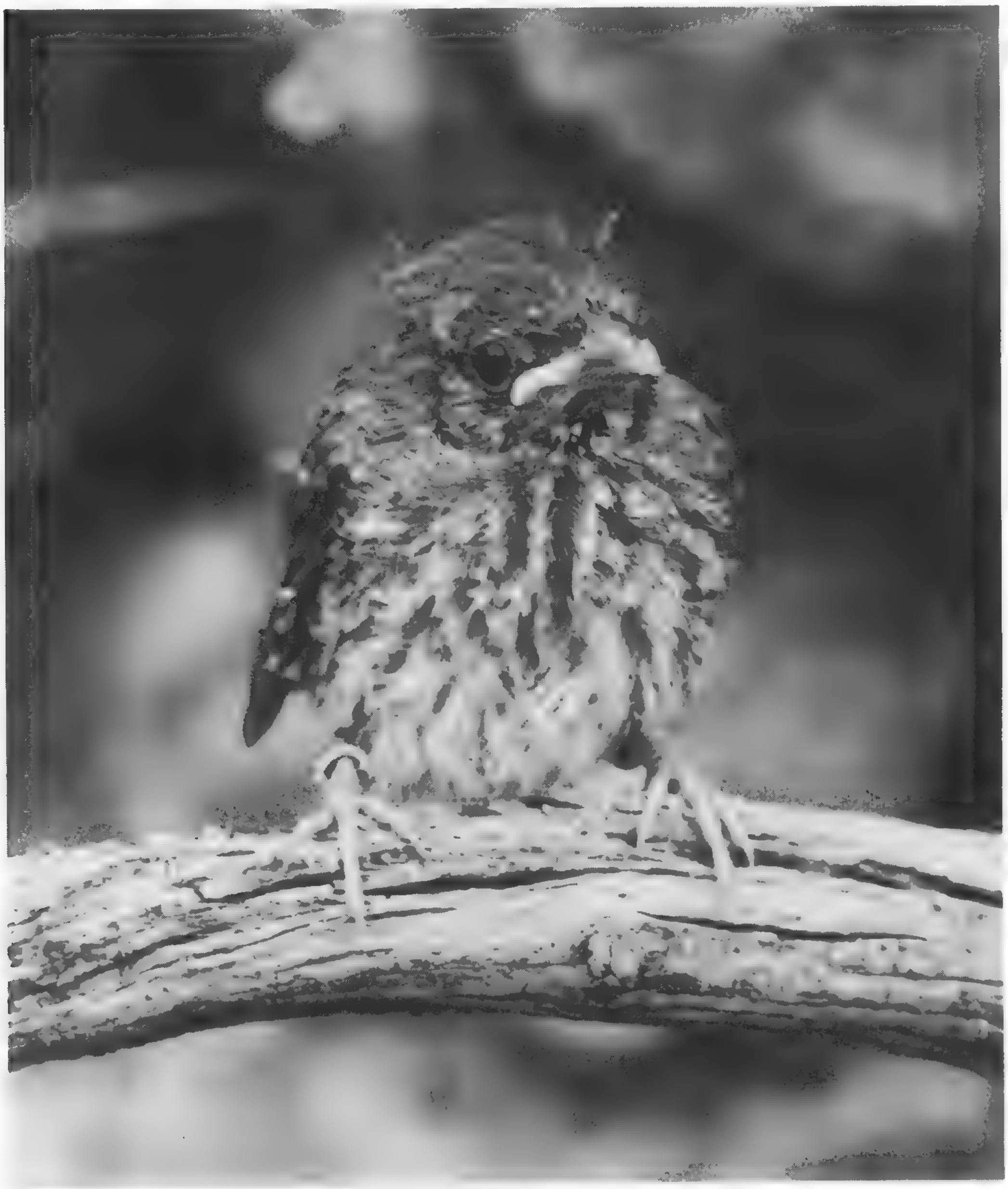


Figure 4. Nine-day-old Five-striped Sparrow just after leaving the nest.

(Aphelocoma ultramarina). Twice we recorded reactions to hawks. An adult and three large young froze and then moved into cover and scolded when an immature Red-tailed Hawk *(Buteo jamaicensis)* sailed less than four meters overhead. An adult male dove into cover and made high-pitched alarm notes when a Cooper's Hawk *(Accipiter cooperi)* flew over.

Of 25 nests observed, 3 never contained eggs, 8 successfully fledged at least one sparrow, 1 fledged only a cowbird, 1 was destroyed in a flood, 6 were apparently robbed by predators, and the outcome of 6 nests was unknown. In two successful nests, one egg or nestling disappeared before three other young fledged.

When nests contained eggs or small young, adult Five-striped Sparrows reacted to human intruders by slipping away quietly or scolding from a nearby shrub. When large juveniles or recent fledglings were molested, as when being banded, adults reacted more intensely; they came to the young, often to within one meter, extended the wings (Figure 5), and hopped around on the ground chattering incessantly. This reaction was triggered by alarm calls from the young; if young remained quiet, the adults were content to scold from a nearby shrub. Males generally reacted with greater intensity than females. In one case, a female gave an intense defense display for some time until the male appeared, at which time she watched quietly from a distance while the male displayed. We subsequently observed a similar defense reaction and posture by Rufous-crowned Sparrows when nests with large young or fledglings were disturbed.

Brown-headed Cowbirds laid eggs in five of twenty-two sparrow nests that contained eggs. Four nests contained one cowbird egg and one contained two. At Patagonia only one of ten nests in 1975 and 1976 was parasitized, but four of six nests were parasitized in 1977 and 1978. We removed cowbird eggs from two nests, predators apparently took all the eggs from one nest, and cowbirds fledged from two nests. One of the nests from which a cowbird fledged also fledged a sparrow. Two sparrow eggs in one of the parasitized nests and one in the other failed to hatch.

Food and Foraging

Wolf [*12*] gives an excellent description of the foraging behavior of Five-striped Sparrows. We noted, as did he, that this species forages primarily on the ground or low in shrubs, which were mostly mesquite and acacia at Patagonia. When on the ground, Five-striped Sparrows foraged mostly under shrubs, but they also foraged frequently in open areas. They picked up food from the ground or branches of shrubs. Five-striped Sparrows move very deliberately compared to Rufous-crowned Sparrows or Rock Wrens, mostly moving at a rate of 1.5 to 2.0 meters per minute. During foraging, they often stopped and scanned the ground and foliage much like vireos. We never observed them scratching in ground litter. On three occasions we saw birds fly off a perch after flying insects.

During the summer, when we watched Five-striped Sparrows most often, food consisted almost entirely of insects, primarily various lepidopteran larvae (Table 4). These were also the primary food fed to young, but grasshoppers became an important food item later in the summer (Table 4). Adults occasionally fed on moths which they chased along the ground after they had been flushed. On two occasions Five-striped Sparrows picked at spider webs, apparently taking insects that had been trapped. In May, June, September, December, and January, and occasionally during other months

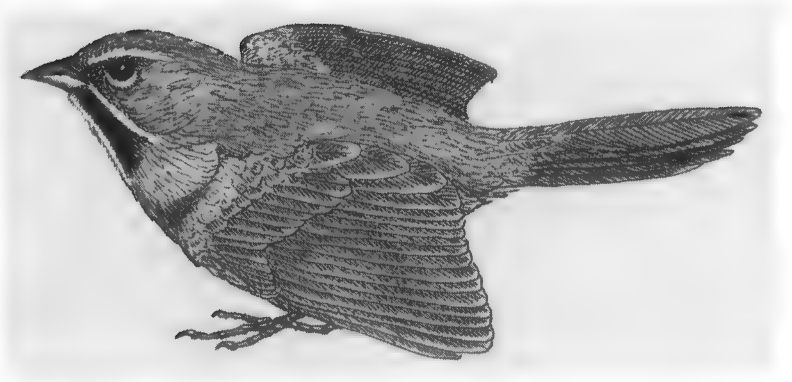


Figure 5. Distraction display of the Five-striped Sparrow given when older young are disturbed. In some cases, the wings are fully extended as the bird hops about and chatters.

of the summer, we saw sparrows feeding on seeds, including those of grass *(Setaria* sp.). We once saw a bird picking up and mandibulating the bases of fallen flowers of chuparosa *(Anisicanthus thurberi).*

Fall and Winter Behavior

Five-striped Sparrows were extremely inconspicuous and elusive from late September to April. Birds usually remained on the ground beneath dense shrubs and rarely ventured into open areas as they did in summer. If pursued, they usually ran along the ground or made short, low flights within patches of dense cover. When forced to fly long distances, they nearly always landed in, or beneath, a dense shrub. The only vocalizations made in the fall and winter were an occasional chatter when disturbed and a high-pitched *seeet* note (probably the *tzit* or *tziiit* described by Wolf[*12*]). The latter call was indistinguishable, or nearly so, from a call given by Rufous-crowned Sparrows. Our few observations suggested that Five-striped Sparrows foraged in winter much the same as in summer but even more deliberately. They spent long periods foraging in small areas; Groschupf watched one bird foraging in an area of less than one square meter for over two hours. During this time it picked at leaves, but whether or not it ate plant material or insects on the leaves is not known.

TABLE 4

Summer Foods of Adult and Young Five-striped Sparrows in Arizona

Type of food	*Food eaten by adults*		*Food fed to young*	
	Number of sightings	*Percentage*	*Number of sightings*	*Percentage*
Caterpillars	27	53	24	56
Grasshoppers	0	—	16	37
Moths	6	12	2	5
Seeds	9	18	0	—
Ants	2	18	1	2
Flying insects	3		0	—
Insects from spider webs	2		0	—
Hackberry fruit	1		0	—
Anisicanthus flowers	1		0	—

In the winter, Five-striped Sparrows sometimes flushed from the ground in the vicinity of other ground-feeding birds such as Green-tailed Towhees *(Pipilo chlorurus)*, Brown Towhees, and especially Rufous-crowned Sparrows, suggesting the formation of loose flocks. There were never enough Five-striped Sparrows present in fall or winter at Patagonia to determine if intraspecific flocking occurred.

Summary

We studied the status, population dynamics, and breeding biology of the Five-striped Sparrow *(Aimophila quinquestriata)* in the United States from 1974 through 1978. Most of the study was conducted near Patagonia, Arizona but we also made observations of five other Arizona populations.

The number of adult Five-striped Sparrows at Patagonia varied from two to ten from 1974 through 1978. Numbers of banded birds that returned in successive years also varied widely. This species appears to be migratory in the United States, leaving the breeding areas most winters. Five-striped Sparrows are extremely elusive and inconspicuous in winter. However, in the winter of 1977–78, at least two birds overwintered at Patagonia and two others were found on Christmas bird counts at other locations in Arizona.

Five-striped Sparrows form stable monogamous pairs and males defend territories. Most territories are on steep hillsides and include, or border, a wash. Territory size ranged from .6 to 2.6 ha but activities were usually concentrated around a nest.

The nesting season extends from early June to mid-September and most pairs nest more than once in a season. Nests are deep cups constructed of grass stems and blades and lined with fine grasses and sometimes hair. Nests were usually built in shrubs but also in grass clumps and the bases of octillos *(Fouqueria splendens)*. Most nests were less than one meter above ground. The success or failure of a nest appeared to influence the placement of successive nests within a territory.

Eggs of Five-striped Sparrows are dull white and unmarked. Females usually laid a clutch of three eggs in early summer and four in late summer. Brown-headed Cowbirds *(Molothrus ater)* parasitized 5 of 22 nests. Incubation lasted twelve to thirteen days and was accomplished solely by the female. Both adults fed the young, which usually left the nest in nine or ten days. Fledglings are cared for solely by the male if the female renests.

The primary food of adults and young was caterpillars. Grasshoppers were also fed frequently to the young, but we never saw adults eating grasshoppers.

Acknowledgements

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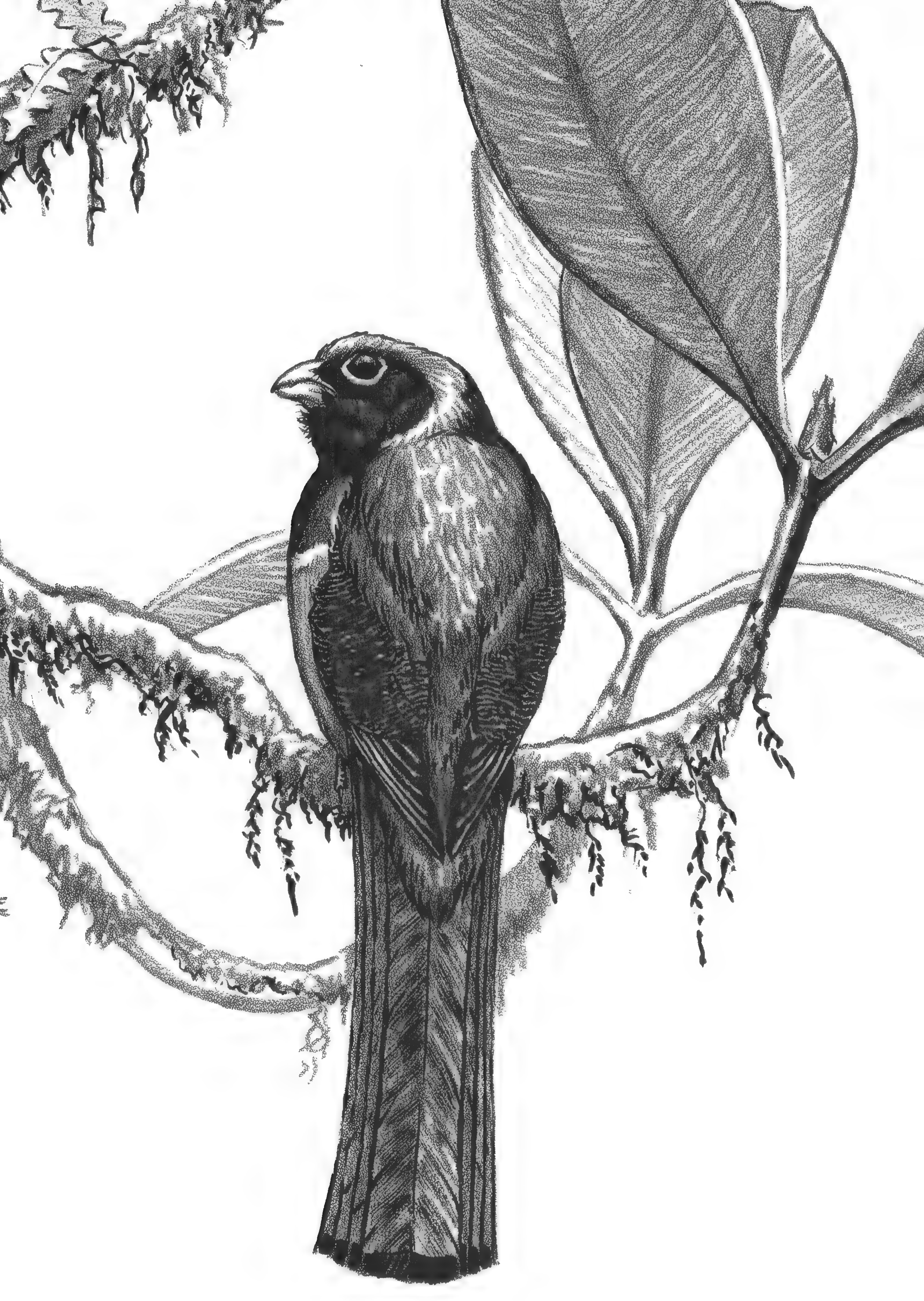
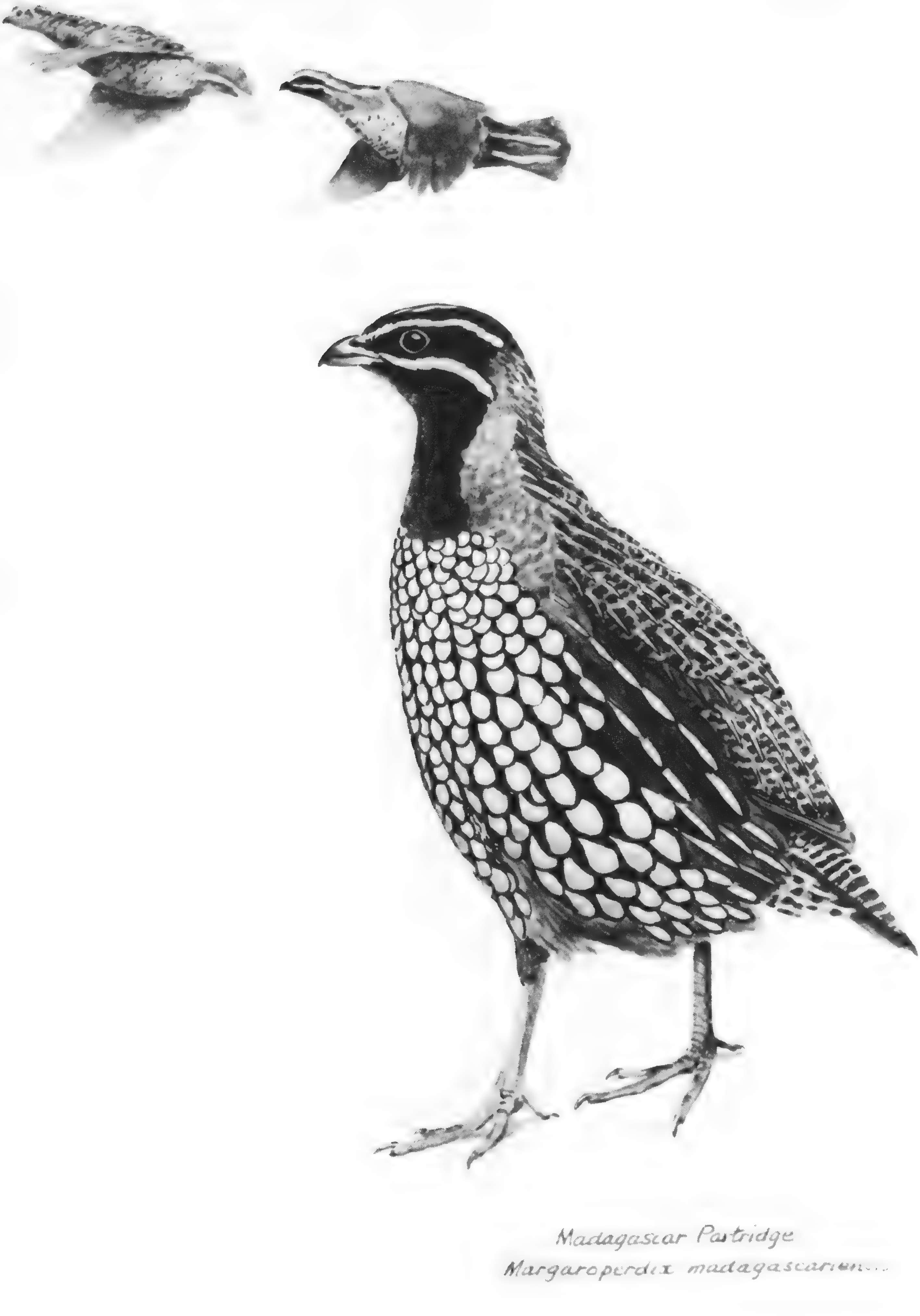


Masked Trogon, *Trogon personatus*. Drawing by James Coe.


Madagascar Partridge
Margaroperdix madagascarien...

Madagascar Partridge, *Margaroperdix madagarensis*. Painting by Terence Shortt.

THE EVOLUTIONARY BIOLOGY OF KINGFISHERS (ALCEDINIDAE)

C. HILIARY FRY

Because kingfishers are not numerous in either the New World or the Palaearctic, western ornithologists have paid rather scant attention to a family of birds which is large and diverse. It is not altogether unexpected that little more is known about some species, that occur only in deep rain-forest in under-explored New Guinea, than that they are nocturnal (the Hook-billed Kingfisher, *Melidora macrorhina*) or habitually dig with their bills into soil in search of earthworms (the Shovel-billed Kingfisher, *Clytoceyx rex*). What is surprising is that the 86 species have escaped evolutionary analysis; for kingfishers have been chosen more than once to illustrate the evolution of "diverse forms of clearly common descent . . . a distinctive and geographically widespread family . . . [with] well marked plumage patterns" [*102*].

In the wake of Sharpe's monograph of the family [*90*], in some copies of which J. Murie's long paper "On the anatomy of kingfishers" appeared, a number of ornithologists conducted basic morphological investigations of the group between 1870 and 1912 [*3, 17, 69, 71, 92, 93*]. A few studies appeared subsequently dealing with the retina [*57, 110*], foot [*98*], skull [*9, 79*], and molt [*99, 111*]; but comprehensive information of the comparative anatomy of kingfishers is still wanting. Some sporadic inquiries on systematics and zoogeography were carried out [*58, 59, 60, 61, 66, 87, 104*], but through lack of knowledge — particularly from the field — interest in kingfisher evolution largely withered. However, the systematic rearrangements of Peters' treatment [*78*] by Wolters [*109*] and Devillers [*20*] brought the matter under scrutiny once more, and with the fresh observations on the biology of kingfishers gleaned in recent decades and the many field studies in progress, this review of the family, with deductions about its geographical and evolutionary radiation, may be timely.

Outline of the Family

Miller [*69*] gave sound reasons for recognizing three subfamilies and his scheme has been widely adopted; but within each subfamily, generic limits are somewhat controversial. My classification in the following review takes cognizance of the morphological criteria established by Miller and others, but I have placed greater emphasis on biological characters.

Subfamily Daceloninae

These medium to very large arboreal kingfishers with 55 species are centered in the region from Indochina to the Bismarck Archipelago and the Coral Sea, i.e. Malesia (Figure 1). Most species are not fishers at all, but are generalized predators of small animals with generalized or in some cases highly specialized means of foraging for them. They inhabit rainforests, woodlands, mangroves, and seashores, nest in tree-holes, and have loud, ringing calls. I recognize eight genera: *Actenoides* (formerly *Halcyon*) with six ornate kingfishers in Malesian rainforests; *Tanysiptera* including six paradise kingfishers in New Guinea; the monotypic *Cittura* in Sulawesi (= Celebes), *Melidora* and *Clytoceyx* in New Guinea, and *Lacedo* from Thailand to Java and Borneo; *Dacelo* with the four kookaburras of New Guinea and Australia; and *Halcyon* (including *Pelargopsis*) with 35 species.

The Australian Laughing Kookaburra (*Dacelo gigas*, or strictly *D. novaeguineae*, which is a misnomer; see Mees [*68*]) is the largest member of the family. It weighs 350 to 500 grams, is the size of a crow, and is a hook-billed predator of land vertebrates. In the large genus *Halcyon*, a few species stand systematically isolated but the remainder fall into one of two distinctive subgenera. One, subgenus *Todiramphus*, is a complex of rainforest and seashore halcyons in Malesia (= Indochina, Indonesia, Malaysia, and New Guinea), Australia, and Polynesia; only one representative ranges west of Malesia, the Mangrove Kingfisher *(Halcyon chloris)*, and it spans half the world with nearly 50 races from Samoa to the Red Sea. Ecological extremes in this group include the small, flycatching halcyons of Polynesia, the offshore-fishing Beach Kingfisher *(H. saurophaga)*, and a bird found across the arid savannas of the Australian interior, the Red-backed Kingfisher *(H. pyrrhopygia)*. The other, subgenus *Halcyon*, embraces the African and several Asiatic halcyons, vocal and strongly territorial inhabitants of woodland, fields, and gardens, and sufficiently conspicuous to have earned a place in folklore.

Subfamily Alcedininae

This subfamily includes very small to medium rainforest or waterside birds with 22 species (Figure 1) in three genera: *Ceyx* (eight dwarf kingfishers, mainly Malesian, the smallest less than 10 grams), *Corythornis* (three small Afrotropical birds), and *Alcedo* (11 species mainly of Malesian forest waterways but also in Australia, the Afrotropics, and the Palaearctic). *Ceyx* feeds mainly on land, *Alcedo* almost entirely from water, and *Corythornis* takes aquatic and terrestrial prey (insects, frogs, etc.) about equally, and is also intermediate morphologically between *Ceyx* and *Alcedo*. Each genus has a representative in open tropical savannas or temperate-zone habitats. They all excavate nest-holes in earthen banks, and have weak, monosyllabic voices.

Subfamily Cerylinae

These small to very large fishers include nine species in three genera. They are the only kingfishers in the Americas, where *Chloroceryle* (the four green kingfishers) is endemic. *Megaceryle* has one Nearctic species, the Belted Kingfisher *(M. alcyon)*, one Neotropical, one African, and one Oriental. The Pied Kingfisher *(Ceryle rudis)* is Palaeotropical, and the cerylines are conspicuous by their absence from the very region, Malesia, where the rest of the family is so abundantly represented. Several species are exclusively piscivorous, and fish from hovering flight. Biologically the cerylines are hardly distinguishable from the larger species of alcedinines, but morphologically they are fairly distinctive [*69*]. The molt patterns of cerylines resemble those of alcedinines [27] more than some [*99*] thought. By minutely-detailed analysis, Miller [*69*] showed that the Amazon Kingfisher *(Chloroceryle amazona), Ceryle rudis,* and the genus *Megaceryle* are about equidistantly related with each other, and that the three smaller species of *Chloroceryle* are morphologically intermediate between those cerylines and the alcedinines.

Feeding Specializations

Within the coraciiform assemblage to which the family Alcedinidae belongs, some families, the insectivorous predators, are apparently generalized in diet and foraging behavior — the motmots (Momotidae), trogons (Trogonidae), and rollers (Coraciidae). Others are specialized, often highly so, like the flycatching todies (Todidae), the bee-eaters (Meropidae), the fruit-picking hornbills (Bucerotidae), the chameleon-eating Cuckoo-roller (Leptosomatidae), and the bark-gleaning woodhoopoes (Phoeniculidae). A similar latitude is evident among the kingfishers. Most of them are generalized predators in forest, with a predilection for watery habitats, eating a wide range of invertebrates and vertebrates taken from both land and water. They are quite unspecialized in their foraging behavior, and catch animals on the ground or at the surface of shallow water simply by swooping down and seizing them in the bill — kingfishers' legs are far too short for manipulative use — and immobilizing or dismembering prey by beating it against the ground or a perch. Others, by contrast, are variously specialized as robust predators of land vertebrates, soil-foragers, earthworm-eaters, sallying flycatchers, and as plunge-diving fishers in particular. The last have a retina evidently adapted for underwater vision, and are likely to have additional structural adaptations [*9*]. General predation on a variety of vertebrate and invertebrate animals likely preceded specialized predation on fish [*37*]. I therefore view exclusively piscivorous kingfishers as being in general more advanced or derived than those preying on a wide range of terrestrial (and aquatic) animals, a view that finds strong support in phylogenetic deductions arising from kingfisher zoogeography.

Breeding Biology

Nests of a few species of kingfishers have not yet been found and detailed accounts of breeding biology have been published for less than a dozen species. From what is known of those and of the bulk of the remaining species of which we know only the bare essentials, breeding biology appears to be uniform throughout the family. Rather than multiplying similar observations in the species review, I have therefore drawn a general account mainly from eight sources [*19, 30, 72, 77, 82, 95, 96, 103*].

Kingfishers are territorial and monogamous. Some *(Actenoides, Lacedo pulchella, Dacelo,* Papuan halcyons, and cerylines) have more or less marked sexual dimorphism of plumage, suggesting some reproductive asymmetry and limited polygamy; yet *Dacelo gigas, Megaceryle alcyon, M. torquata, M. rudis,* and *Chloroceryle amazona* are certainly monogamous. Territorial display by loud singing and conspicuous wing-spreading characterize some African and Asiatic *Halcyon* species; other dacelonines have loud songs, but postural displays have not been described. Unobtrusive but structurally complex warbling songs characterize *Chloroceryle, Alcedo atthis,* and *Corythornis cristatus*.

Kingfishers nest solitarily or in loose colonies, the most colonial being the

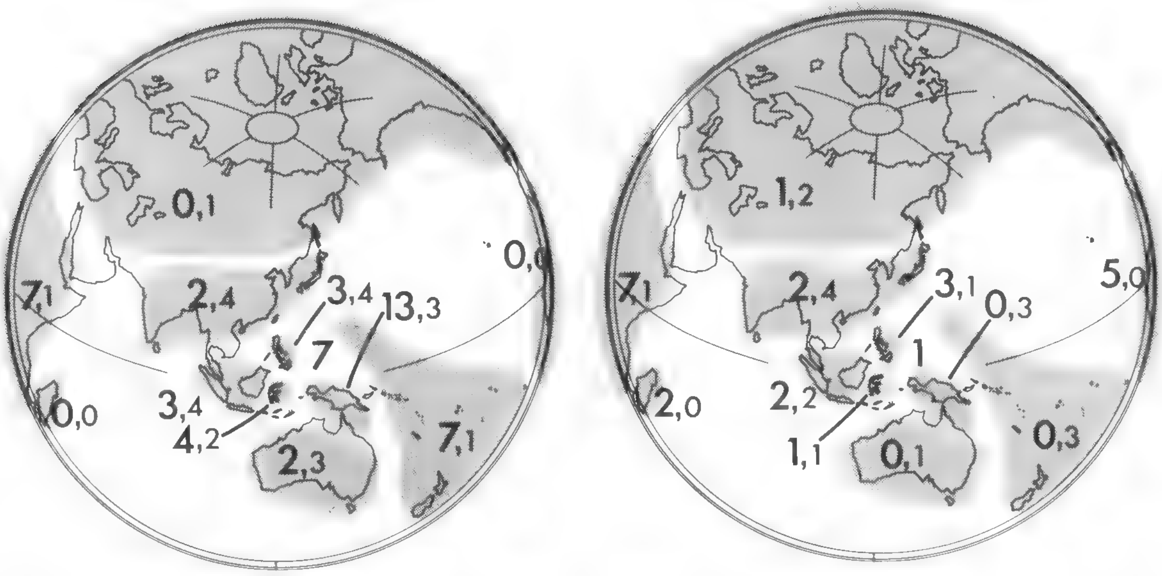


Figure 1. Regional distribution of species of kingfishers, subfamily Daceloninae in the left figure and subfamilies Alcedininae and Cerylinae in the right. Bold numbers represent the number of endemic species in a given region. Small numbers indicate the number of non-endemic kingfishers occurring in the region. The bold number **7** in the left figure and number **1** in the right, north of New Guinea, refer to island endemics not in any of the regions as delineated: *Halcyon fulgida, H. diops, H. lazuli, H. albonotata, H. funebris, H. saurophaga, H. australasia*, and *Alcedo websteri*.

Pied Kingfisher, which also breeds communally with up to four or five helpers at the nest. Africa's Striped Kingfisher *(Halcyon chelicuti)* and Australia's Laughing Kookaburra also have helpers. Alcedinines excavate their own nest holes in earth banks near water, occasionally up to a kilometer away. Using the bill, they loosen the soil and kick it out with the feet. The tunnel is horizontal, straight, or a little curved, 0.75 to 1.5 meters long, and ends in an oval egg chamber. Dacelonines nest in tree holes, often expropriating them from other birds and remodelling the chamber, and they commonly use holes in termitaria on the ground or high in trees. Some, notably the African and Asiatic halcyons, regularly nest also in earth banks, excavating the tunnel themselves. Kingfishers never line the nest chamber.

Eggs are white and subspherical. Incubation begins with the first egg laid. The sexes incubate alternately in a cycle varying from about three hours in the Half-collared Kingfisher *(Alcedo semitorquata)* to 24 hours in the Amazon Kingfisher *(Chloroceryle amazona)* with the female incubating all night, and even 48 hours in the Ringed Kingfisher *(Megaceryle torquata)* with each sex taking 24-hour spells of incubation. During incubation the egg chamber becomes fouled with pungent, watery excrement and trodden-down pellets of regurgitated insect sclerites or fish bones. The process accelerates after the eggs hatch, when the nest acquires a characteristic stench of ammonia; dipterous and coleopterous larvae inhabit the debris. Clutches vary from one egg (rarely in *Dacelo gigas*) to ten (rarely in the Eurasian Kingfisher, *Alcedo atthis*), with means of about three to four eggs in tropical kingfishers and six to seven in species of the temperate zone. Many kingfisher species lay second, and replacement, clutches.

On hatching, the young break off the shell cap (blunt end), which is oblique and irregular, differing from the condition in all birds other than the allied trogons and bee-eaters. The hatchling is prognathous, the mandible projecting up to 2.5 millimeters beyond the maxilla, until redressed about a week later by the faster growth of the maxilla. Nestlings are naked at first, and graded in size according to hatching sequence. The youngest, smallest members of the brood frequently die and are trodden into the litter of the nest chamber. Adults provide nestlings with a diet similar to their own. Nestlings become feathered with a plumage that is almost indistinguishable from the adult female's within several weeks after fledging, except in those with characteristically melanized plumages (*Tanysiptera*, some Papuan halcyons, and *Corythornis*). Adults continue to feed young birds out of the nest for an unusually long time, up to at least ten weeks. After the breeding season, many kingfishers become essentially solitary, but others, although seldom gregarious, continue living in a family party which, in *Dacelo gigas*, has an elaborate social structure and defends a group territory.

REVIEW OF THE SPECIES

Subfamily Daceloninae

Genus *Actenoides* (Figure 2, Plate 1)

This ornate genus comprises three species plus a superspecies (Figure 2) of three allospecies; that is, three geographically separated species that are so similar they are obviously of common origin not long ago, yet are too different to be included in a single species. Actually, members of this superspecies often are treated as conspecific, as one species. Nearly all authors have placed them in *Halcyon*, but they look sufficiently different from other halcyons and have enough common characters among themselves to warrant generic separation. I arrived at this view independently of Wolters [*109*], who also segregated them (as *Actenoides* Bonap., 1850, with *A. bougainvillei incertae sedis*). All species inhabit the deep interior of rainforests, the rare and little-known Moustached Kingfisher *(A. bougainvillei)* being restricted to Guadalcanal and South Bougainville in the Solomon Islands and hence not in Malesia as defined here. While we know little more about the two Sulawesi species than about the Solomons bird, they all seem to be quiet, rather stolid birds with heavy flight, feeding on large beetles and millipedes *(A. monachus)*, cicadas, cockchafers and longicorn beetles, ants, and occasionally fish *(A. concretus,* [*97*]*)*. They live well away from water and range in altitude to about 900 meters, or in the case of *A. princeps* from 900 to 2,000 meters. They nest in tree holes and rotten stumps.

Ecologically these birds seem to be typical halcyons. Morphologically, however, all species of *Actenoides* are sexually dimorphic in plumage (Plate 1). Dimorphism is most pronounced in the *A. concretus* superspecies with its buff and dark blue males and buff-spotted olive green females. The female *A. monachus* (Figure 2) has a dark blue head, rufous underparts, rufous eye line, and olive green back, wings, and tail. The male differs in having an all-blue head. *A. princeps* lacks green or rust in the plumage; the female's blue and buff head is like the female of *A. monachus*, and the male's is also all-blue. Both sexes of *A. bougainvillei* are rufous, with deep blue wings and tail, but the scapulars are deep blue in the male, olive in the female. The geographical separation of *A. bougainvillei* from the others suggests a distant kinship. Its plumage is quite like the Torres White-tailed Kingfisher *(Tanysiptera sylvia)*, some specimens of which even have the olive wash on the scapulars, and it forms a link between the genera *Actenoides* and *Tanysiptera*.

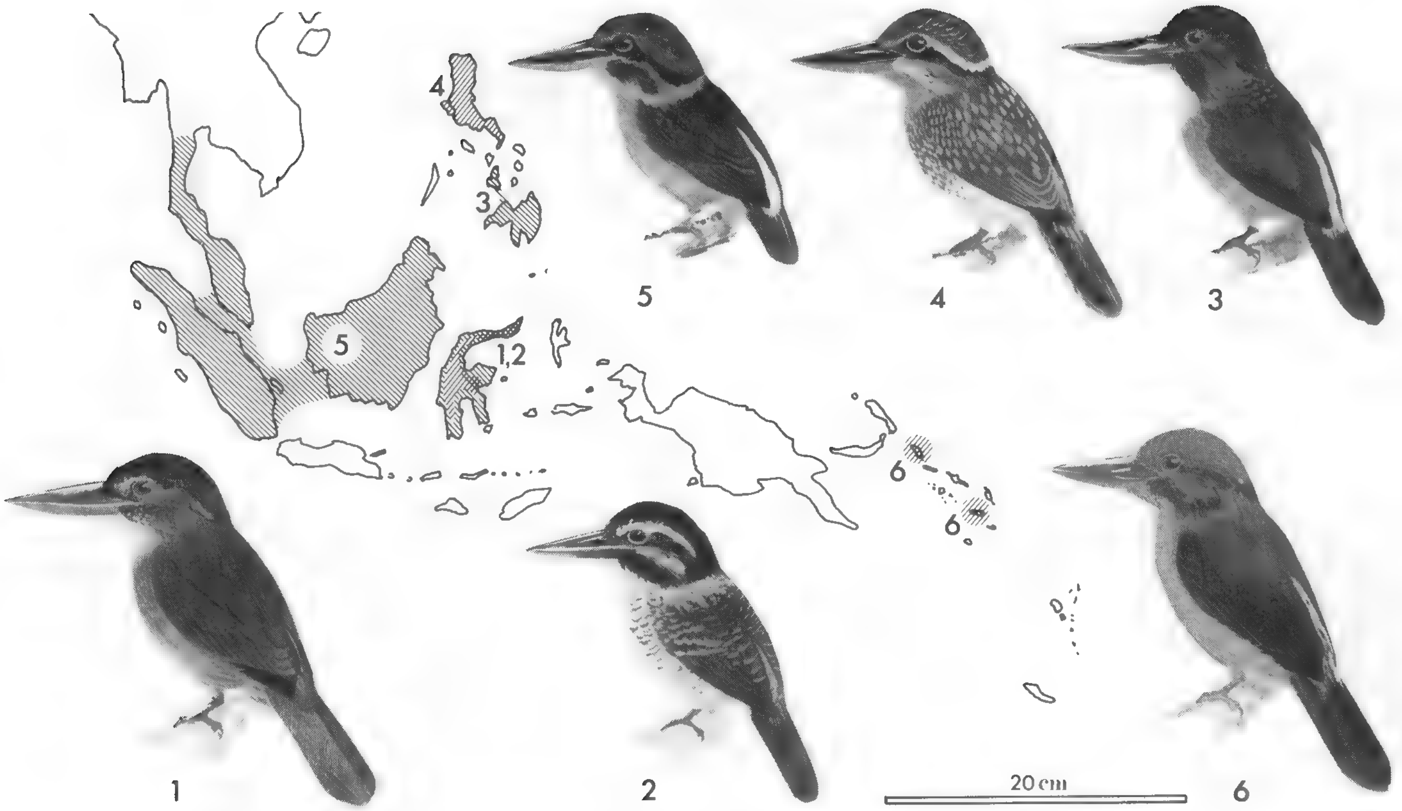


Figure 2. Distribution of the genus *Actenoides* **1**, *A. monachus*, Celebes Green Kingfisher, ♀ *(3)*; **2**, *A. princeps*, Celebes Mountain Kingfisher, ♀ *(3)*; **3**, *A. hombroni*, Hombron's Wood Kingfisher, ♂ *(monotypic)*; **4**, *A. lindsayi*, Spotted Wood Kingfisher, ♂ *(2)*; **5**, *A. concretus*, Rufous-collared Kingfisher, ♂ *(2)*; **6**, *A. bougainvillei*, Moustached Kingfisher, ♀ *(2)*. Species **3, 4**, and **5** constitute a superspecies. In most kingfishers the sexes are barely distinguishable in appearance. When they differ markedly, the sex of the bird portrayed is indicated following the common name. The italicized numbers in parentheses indicate the number of races or subspecies that exist for that species. Birds in Figures 2, 3, 5, 8, 15, and 21 are drawn to the scale shown in Figure 2; those in Figures 4, 9, 10, 11, 14, 17, 18, 19, and 20 to the scale shown in Figure 4; and those in Figure 22 to the scale shown there.

Genus *Tanysiptera* (Figure 3)

Recent field studies by H. L. Bell* and B. Coates (unpubl.) have added considerably to the otherwise meager knowledge of the genus *Tanysiptera. T. galatea*, the most widespread paradise kingfisher, occurs more or less commonly in lowland rainforest up to 300 meters in most parts of New Guinea, as well as in the Moluccas and other islands. It is highly sedentary, as shown by banding studies of a population having the extraordinarily high density of 50 birds per 10 hectares [*4, 5*].

It is scarcely surprising, therefore, that populations insulated from the mainland by seas have rapidly differentiated; eleven of the fourteen races are on islands. *T. g. ellioti* of tiny Kofiau Island and *T. g. riedelii* of Biak Island are usually treated as full species; here I treat them as subspecies of *T. galatea* because their plumages and sizes are well within the range of its polytypic variability, and I recognise only one island representative, namely *T. carolinae* of Numfoor Island, as differing in plumage from *T. galatea* sufficiently to warrant specific status.

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*Bell's papers *Information on New Guinean kingfishers, Alcedinidae* (Ibis, in press) and *Seasonality and territorial behaviour of the Common Paradise Kingfisher* Tanysiptera galatea (in prep) have appeared too late for reference in this text.

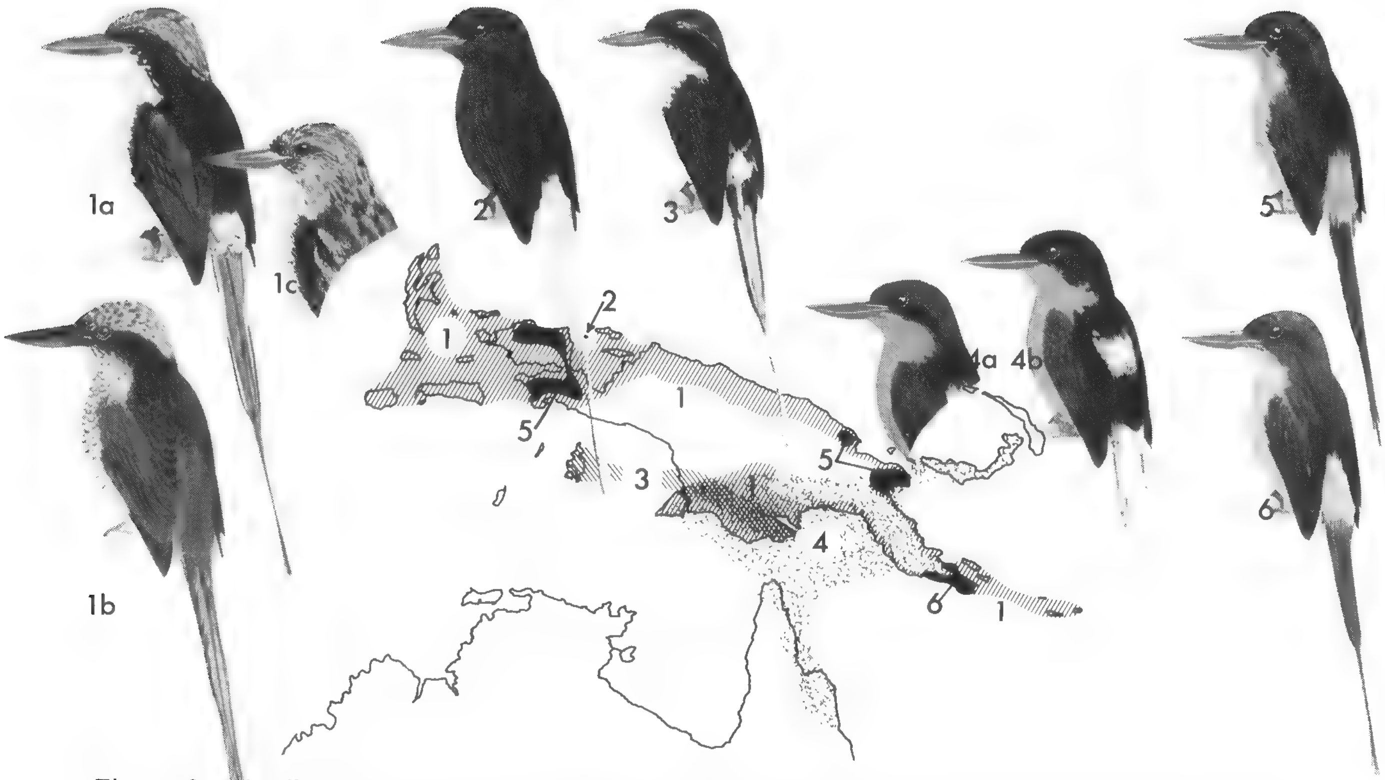


Figure 3. Distribution of the genus *Tanysiptera*. **1**, *T. galatea*, Common Paradise Kingfisher *(14)*; **2**, *T. carolinae*, Numfor Paradise Kingfisher *(monotypic)*; **3**, *T. hydrocharis*, Aru Paradise Kingfisher *(monotypic)*; **4**, *T. sylvia*, Torres White-tailed Kingfisher *(4)*; **5**, *T. nympha*, Pink-breasted Paradise Kingfisher*(monotypic)*; **6**, *T. danae*, Brown-headed Paradise Kingfisher *(monotypic)*. The following races are shown: **1a**, adult *T. g. galatea*; **1b**, juvenile *T. g. galatea*; **1c**, adult *T. g. riedelii*; **4a**, *T. s sylvia*; **4b**, *T. s. nigriceps*. Species **1** and **2** constitute a superspecies; species **5** and **6** another superspecies. *T. sylvia* is called the White-tailed Kingfisher in Australia and the Australian Paradise Kingfisher *(82)* in New Guinea. The vernacular name used here, Torres White-tailed Kingfisher, prevents confusion with *T. carolinae*, which is white-tailed and relates *T. sylvia* with Papua as well as with Australia.

An approachable bird, the Common Paradise Kingfisher spends much time sitting quietly in the lower storey, where it draws attention to itself by raising and depressing the elongated tail with its conspicuous spatulate white tip — a generic feature — through 90 degrees. It hunts mostly within two meters of the ground in the wet season (higher in the dry), darting out to seize earthworms, caterpillars, and a variety of other insects. In the breeding season this kingfisher becomes even more conspicuous, as each pair vigorously defends its small territory from neighbors. This species nests in tree holes and termitaria and lays a clutch of five eggs.

In strong contrast with the usual condition of tropical rainforest birds, the Common Paradise Kingfisher has a high breeding success. Toward the end of the wet season, the abundant brown juveniles are forced into marginal habitats — secondary forest growth and patches of scrub in open savanna — they evidently experience a high mortality since recruitment is very low [*6*]. Juveniles of all species of *Tanysiptera* are much duller-plumaged than adults; the juvenile of this species, for instance, has brown back and wings (blue in the adult) and scaly buff underparts (white in adults). Its cap is light blue like the adult's, its tail is dusky with the central rectrices not yet elongated, and the bill is blackish, becoming orange within a year but not red until two years of age.

T. hydrocharis resembles *T. galatea* in plumage and habits but is smaller. The two kingfishers occupy the same habitat in the Fly River area of southern New Guinea [*82*], which *T. hydrocharis* probably invaded after differentiating in the Aru Islands, where it is the only representative of its genus.

The Torres White-tailed Kingfisher *(T. sylvia)* is closely related with *T. galatea*, the main plumage differences being the white back spot and orange (not white) underparts in *T. sylvia*. One subspecies occurs in southeastern New Guinea, where it is rare, inhabiting a narrow belt of forested foothills. Another breeds in rainforest in the Cape York peninsula of Queensland and migrates over the Torres Straits to winter in southeastern New Guinea; and a third inhabits New Britain. All frequent forest canopy, nesting in arboreal termitaria in New Britain and New Guinea and termitaria on or near the ground in Queensland. Feeding in the canopy may help the Queensland population to reduce winter competition with *T. galatea*, which is the same size; the resident New Guinea population probably avoids significant competition with *T. galatea* because of its smaller size (35% lighter).

T. nympha and *T. danae* are pink-breasted and pink-rumped birds with a relict distribution, the former in mangroves and forest up to 1,000 meters and the latter in forested foothills. No nests of either have been discovered. Because of precipitous terrain in poorly-explored easternmost New Guinea where their ranges might overlap, they could be effectively allopatric on either side of a cordillera even if only two kilometers apart [*5*]. We do not yet have the field information to prove that they meet in nature.

Genera *Cittura, Melidora,* and *Clytoceyx* (Figure 4)

Endemic to Sulawesi, *Cittura cyanotis* is common only in the northern peninsula, occuring in primary rainforest up to 1,000 meters. It has been recorded from only three other mainland sites. Another race is found on Great Sangihe and Siau islands to the north. It feeds on large insects and

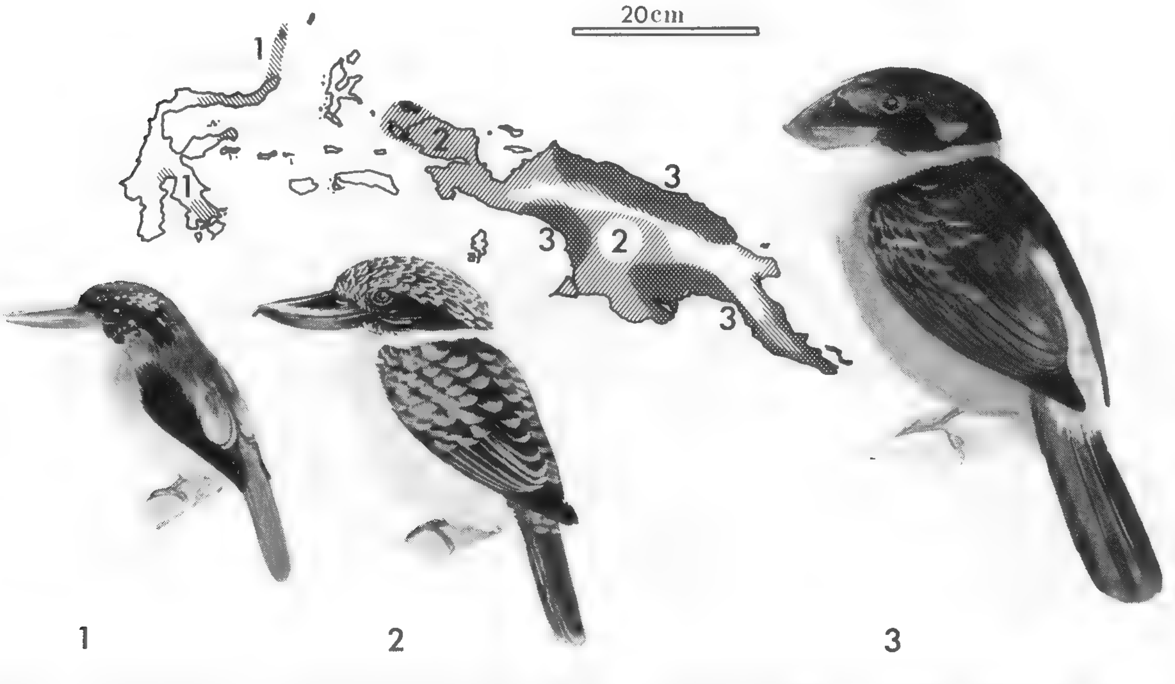


Figure 4. Distribution of the genera *Cittura, Melidora,* and *Clytoceyx*. **1**, *Cittura cyanotis*, Celebes Flat-billed Kingfisher *(3)*; **2**, *Melidora macrorhina*, Hook-billed Kingfisher, ♂ *(3)*; **3**, *Clytoceyx rex*, Shovel-billed Kingfisher, ♀ *(2)*.

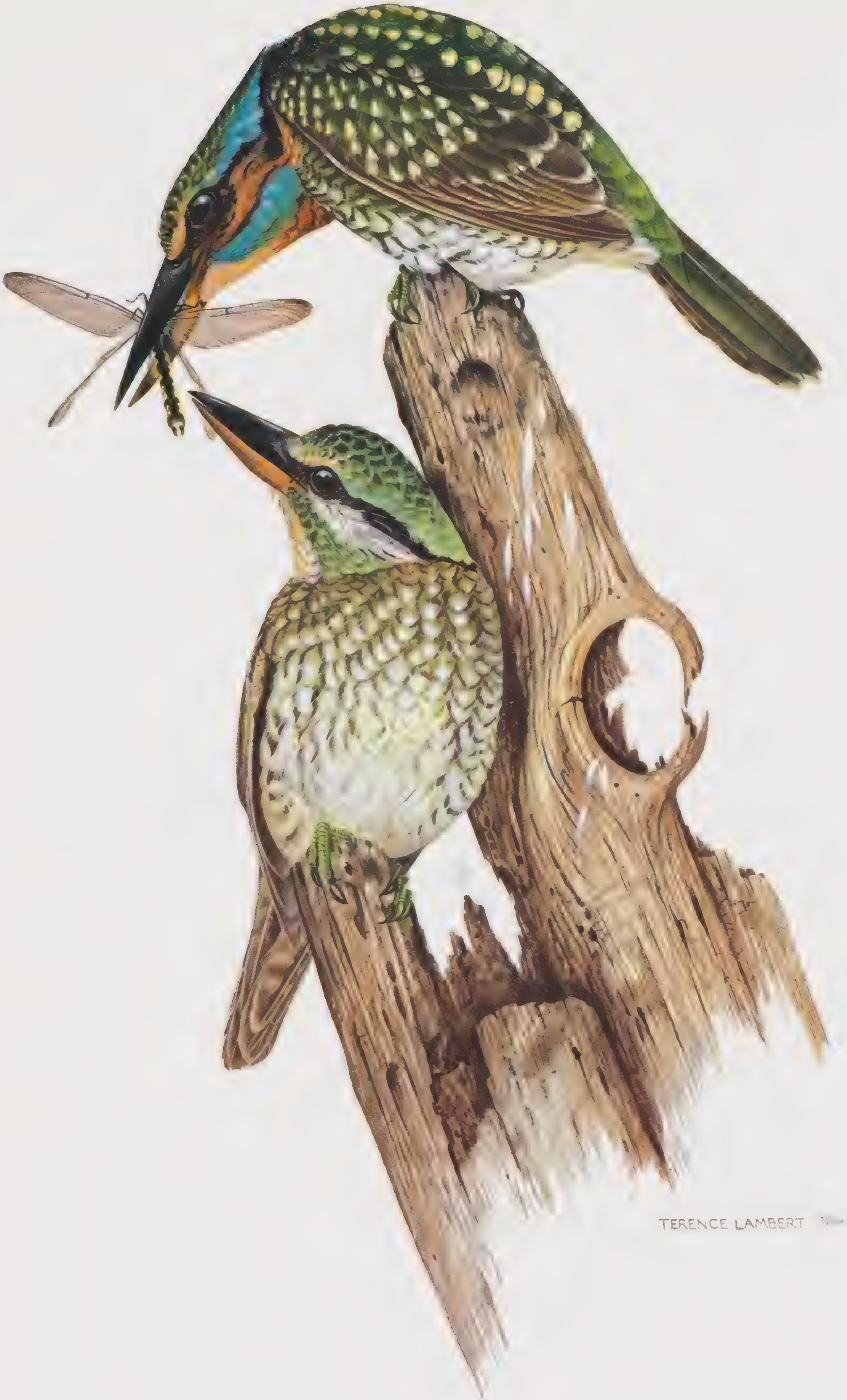

TERENCE LAMBERT

Plate 1. Spotted Wood Kingfisher, *Actenoides lindsayi lindsayi*. **Painting by Terence Lambert.**

millipedes (C. M. N. White, in prep.). Nothing else has been recorded about its habits. Morphologically, its distinguishing features include a dorsoventrally flattened bill, nearly bare lores, and lilac auricular feathers stiffened and sparsely barbed (but not forming a tuft as claimed by C. M. N. White, in prep.). The plumage is unique: brown, with orange tail, dark blue wings and sides of head, and a strong lilac wash.

Even more distinctive is the genus *Melidora*. It has a robust, hooked bill with a wide, grooved culmen, and feeds largely, if not wholly, by night on the floor of the lowland forests it inhabits. It is the only nocturnal coraciiform bird. It occurs quite commonly in parts of New Guinea. During the day it sits quietly in the lower storey and can be approached closely; at night it calls frequently and is evidently active. Rand and Gilliard [*82*] collected one which had the inside of the bill encrusted with mud, as if it had been digging with it, and they quote Ramsay's statement that this bird obtains much of its food by digging with the bill in leaf litter. Insects and a frog have been found in stomachs. The Hook-billed Kingfisher nests in termitaria on forest tree-trunks and has a clutch of two eggs. Rand and Gilliard [*82*] record that both mandibles have egg-teeth and that the nestling has an even more strongly hooked bill than the adult.

Melidora is white below and brown above with black bill and head, the crown feathers of the male being edged with pale blue. The breast is faintly dark-scalloped. I am impressed by its plumage resemblance to the distinctive juvenile of *Tanysiptera galatea* (Figure 3); moreover, the usual call-notes of the two species are similar and the alarm calls are almost identical [*5*]. It is possible that *Melidora* and *Tanysiptera* are of immediate common descent and that the former is a specialized derivative that has retained, in the adult, the ancestral juvenal plumage (a condition called paedomorphosis). That idea could be tested by careful examination of the bill characters of very young *Tanysiptera*.

In another direction *Melidora* has marked resemblances to both the Shovel-billed Kingfisher *(Clytoceyx rex)* and the kookaburras (*Dacelo* spp.). All have uniformly colored underparts with obscurely dark-scalloped breasts and a pale collar; all are large. *Melidora* and *Clytoceyx* share topsoil-foraging and a buff-scalloped brown back. With *Dacelo, Melidora* shares sexual dichromatism and similar bill morphology. If they are all quite closely related, it is tempting to speculate that *Dacelo* evolved "from" *Tanysiptera* by way of forms like *Melidora* or *Clytoceyx*.

Yet another inhabitant of the lowland rainforests of New Guinea, the bizarre Shovel-billed, or Earthworm-eating, Kingfisher does as its names suggest [*5, 22, 82*]: it feeds on the ground, either by pouncing onto such mobile prey as beetles, mice, snakes, and lizards, or by thrusting its bill into soil and working it from side to side for a minute or more at a time; the bird evidently braces itself with its tail. Earthworms are then the main prey, perhaps insect larvae and snails too, all having been found in stomachs. The bird drags out a long worm [*82*], lifting its head in an apparently thrush-like manner. Many museum specimens have caked mud on, or in, the bill, so perhaps "shovelling" is its main mode of foraging.

Clytoceyx occurs up to 2,500 meters but is less commonly encountered than *Melidora*. If it is dependent on exposed, damp earth for feeding, it will be restricted to mid-montane forests, which seems to be the case [*5*]. Breeding has not been described, nor has voice (J. M. Diamond informs me that his voice-figure [*22*] was wrongly attributed). The plumage, brown above with

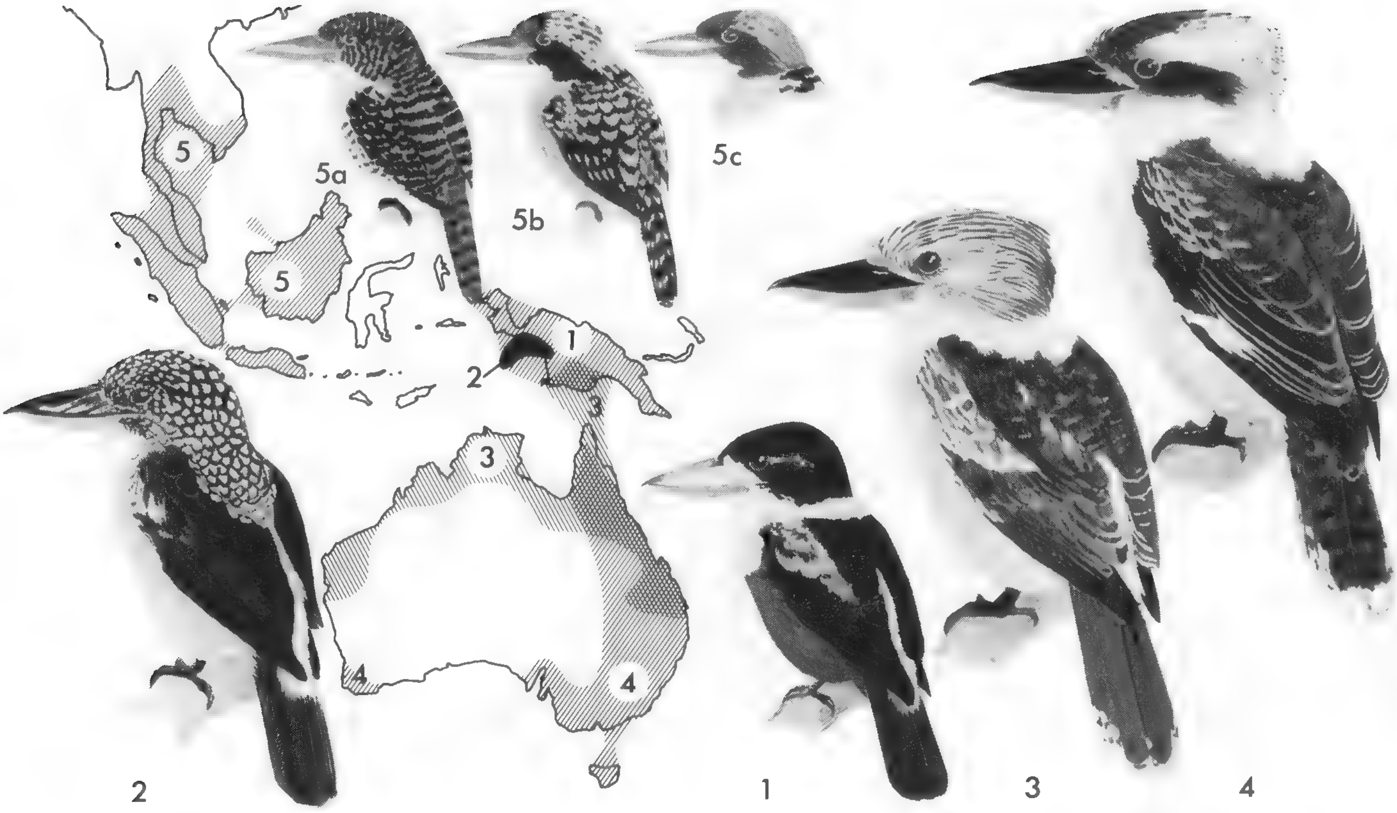


Figure 5. Distribution of the genera *Dacelo* and *Lacedo*. **1**, *D. gaudichaud*, Rufous-bellied Kookaburra, ♂ *(monotypic)*; **2**, *D. tyro*, Aru Kookaburra *(2)*; **3**, *D. leachii*, Blue-winged Kookaburra, ♂ *(5)*; **4**, *D. gigas*, Laughing Kookaburra *(2)*; **5**, *L. pulchella*, Banded Kingfisher *(3)*. The races include **5a**, *L. p. amabilis*, ♀; **5b**, *L. p. melanops*, ♂; **5c**, *L. p. pulchella*, ♂.

blue rump and finely-scalloped ochre below, is like the kookaburras', and two more characters strongly suggest quite close affinity: sexual dimorphism in the tail—blue-black in males and chestnut in females—and vestigial blue in the bend of the wing of occasional examples.

Genera *Dacelo* and *Lacedo* (Figure 5)

The three largest kookaburras are birds of savanna woodlands; only the Rufous-bellied Kookaburra is a forest bird, and unlike the genera considered above it is not restricted to rainforests but also inhabits mangroves, forest edge, secondary growth, and gardens. I have considered each of the four species in turn as a prospective geographical ancestor of the others and (although there is not room to detail the arguments here) can comprehend only *D. gaudichaud* in that role. If that is the most primitive kookaburra, it implies that the genus has evolved from rainforest into savanna habitats, and that it originated in New Guinea and later invaded Australia. Superficially *D. gaudichaud* shows little plumage resemblance to the other three; it is a black and white bird with chestnut belly, sky-blue shoulders and rump, and dark blue (male) or rufous (female) tail. On closer inspection, however, the ochre belly and buff-spotted black head of *D. tyro* can be derived from the chestnut belly and black head with buff collar of *D. gaudichaud*, while *D. leachii* shares with *D. gaudichaud* the blue wings and blue tail of the male and rufous of the female. Although *D. gaudichaud* is solitary and the savanna *D. tyro* and *D. leachii* somewhat gregarious, the three have similar voices, postures, and foraging and nesting behavior. *D. gigas* looks and behaves much like *D. leachii* but is not dimorphic, lacks dark blue, and has a very different voice—the famous laugh.

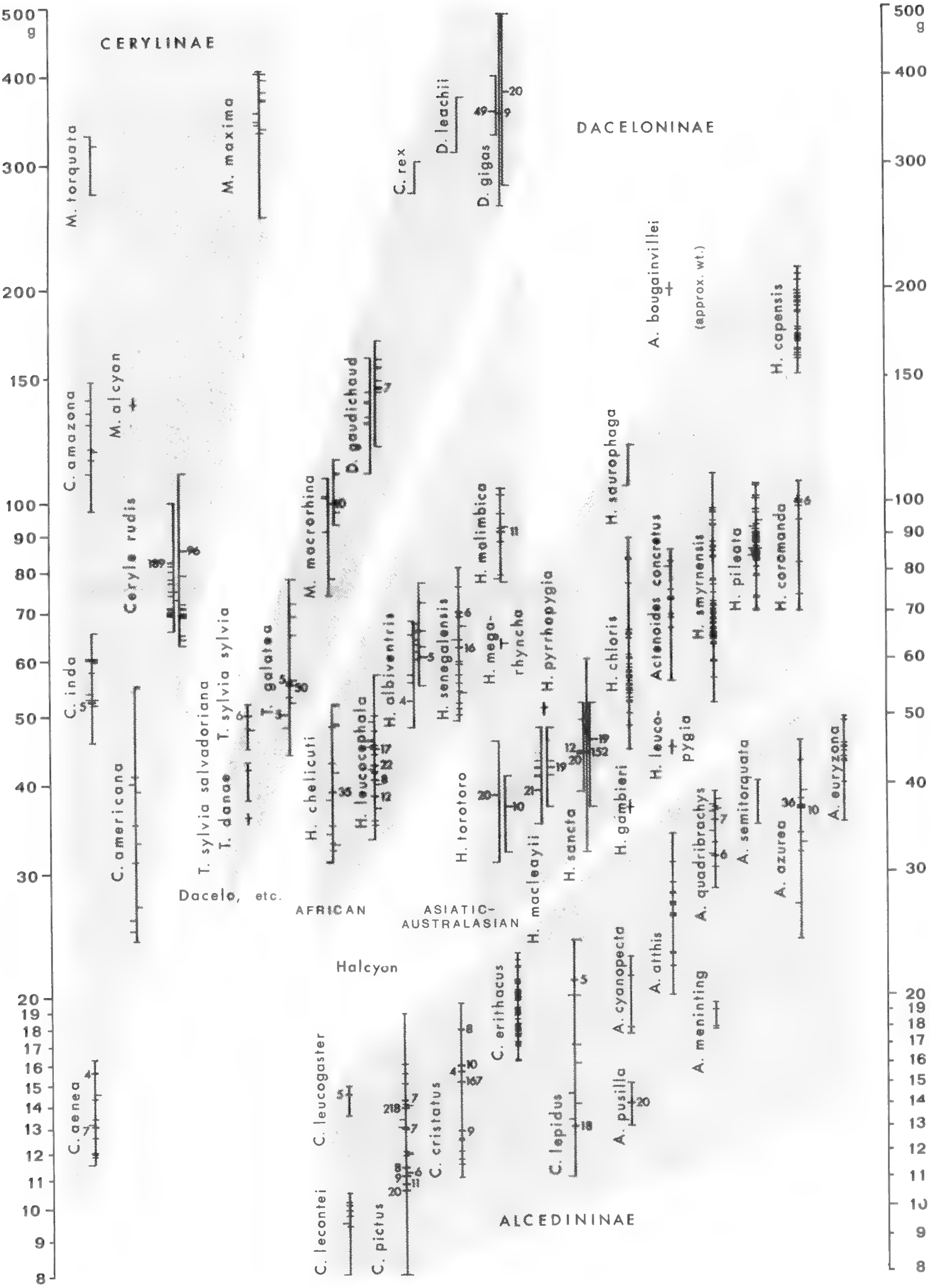
Hypothetically, the evolutionary history of kookaburras is that the ancestral *gaudichaud* produced a Torrean isolate in humid savanna which eventually gave rise to *tyro* on the Aru Islands, from where it subsequently re-invaded adjacent New Guinea. The ancestral *gaudichaud* also gave rise to proto-*leachii*. An invasion of the subtropical and then the temperate-zone woodlands by proto-*leachii* gave rise to *gigas*. In the meantime proto-*leachii* became *leachii* while still in Torrean savannas. The geologically recent recrossing of the Torrean isthmus has stranded a population of *D. leachii* in New Guinea. The Australian population, like its early derivative, is evidently extending southward. These speculations do not differ importantly from Keast's [*54, 55*] conclusions regarding the two Australian species.

Throughout the lowlands of New Guinea and the Aru and Western Papuan islands, the Rufous-bellied Kookaburra is a common and conspicuous bird. It is highly vocal and aggressive in defense of its territories (B. Coates, *in litt.*), nests in elevated tree holes and arboreal termitaria, and lays a clutch of two eggs. It feeds mainly on insects; crabs, lizards, and birds have also been taken [*5*]. The Aru and Blue-winged Kookaburras are similar in these respects, and the former is the only New Guinean endemic land bird confined to natural savanna [*5*]. Laughing Kookaburras are much better known.

Common in east Australian woodlands, often almost a garden bird, the huge Laughing Kookaburra permanently occupies a socially defended territory, is conspicuous as it perches in the open, and "laughs." The best known bird voice in Australia, this song is "like nothing else in nature, the wildest human cachinnation falling short of its glory" [*62*]. When singing, the Kookaburra points its bill skyward and wags its tail up and down. Its mate and any other members of its family group join in. Laughing Kookaburras are sedentary and live as a pair or as a group of three to six adult birds.

Numerous bird species in Australia and throughout the tropics live perennially in social groups, and Parry's [*76, 77*] studies of *D. gigas* show that it is typical of a major category of cooperative or communal breeders. In rather more than half of kookaburra territories, the young birds do not disperse but remain with their parents and are active not only in defense of the territory but also in helping their parents with subsequent broods. At a second nesting in the same season, or one the following year, the helpers incubate the eggs and feed the brood. Fledging success from nests with helpers is nearly twice as high as that from nests without them. Some evidence suggests that *D. leachii* and *D. tyro* are also cooperative breeders [*5*].

Laughing Kookaburras are predators of large insects (33% of food items), lizards and snakes (35%), earthworms (15%), crayfish (8%) and mice, rats, and birds, all seized on the ground [*76*]. Snakes may be dropped from a height to stun them. Prey is not dismembered but is swallowed whole. Kookaburras nest in holes in gum trees where a branch has broken off, and less commonly in arboreal termitaria. Breeding biology has been described and documented by Parry [*76, 77*] and its details agree with what is known of other tree-kingfishers. She noted that 25 adult females (excluding any weighed a month before egg-laying) averaged 15 percent heavier than 26 males and found the difference not significant statistically. With additional data I find the difference is significant; females are heavier on the average than males in a variety of kingfisher species (Figure 6). This species has lost most of the sexual dichromatism of its putative ancestors and its plumage is rather variable; but most females have buff above the eye and brown rumps, and most males have white above the eye and blue rumps.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ALCEDININAE
M. torquata
M. maxima
C. amazona
M. alcyon
Ceryle rudis
C. inda
C. americana
C. aenea
T. sylvia salvadoriana
T. sylvia sylvia
T. danae
T. galatea
Dacelo, etc.
M. macrorhina
D. gaudichaud
C. rex
D. leachii
D. gigas
AFRICAN
ASIATIC-AUSTRALASIAN
Halcyon
H. chelicuti
H. leucocephala
H. albiventris
H. senegalensis
H. malimbica
H. megarhyncha
H. torotoro
H. macleayii
H. pyrrhopygia
H. sancta
H. chloris
H. gambieri
H. saurophaga
A. bougainvillei
(approx. wt.)
Actenoides concretus
H. leucopygia
H. smyrnensis
H. pileata
H. coromanda
H. capensis
A. quadribrachys
A. semitorquata
A. azurea
A. euryzona
A. atthis
A. cyanopecta
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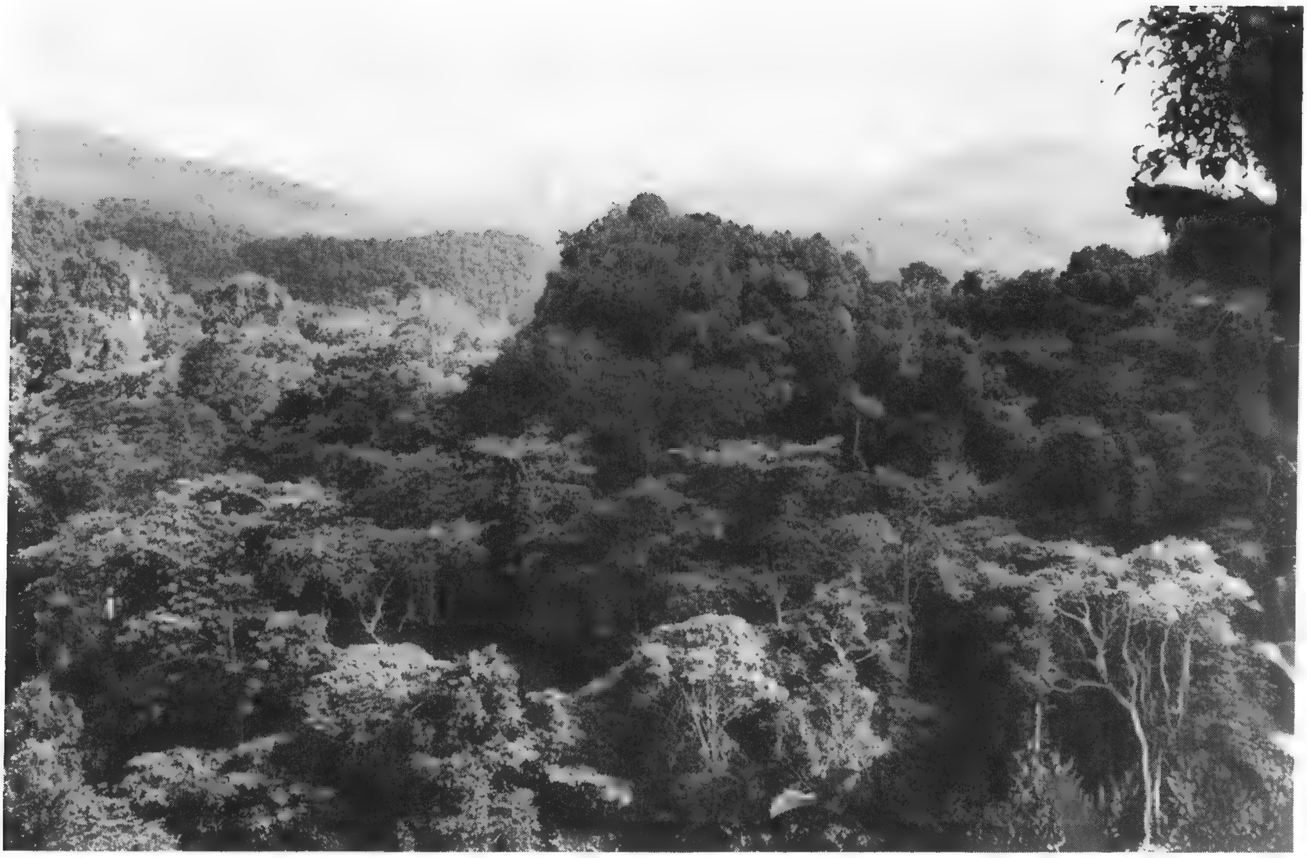


Figure 7. Equatorial lowland rainforest, Mulu National Park, Sarawak (Malaysia), Borneo. Habitat of the Banded Kingfisher *(Lacedo pulchella)*, the Oriental Dwarf Kingfisher *(Ceyx erithacus)*, and others.

Perhaps the Banded Kingfisher *(Lacedo pulchella)* is an early offshoot of the kookaburra lineage, although its range is separated from the kookaburras' by the whole of Wallacea (i.e., Sulawesi, the Moluccas, and the lesser Sunda Islands west to Lombok). It is a lively and vocal resident of primary forest (Figure 7) up to 1,700 meters, and in its large-insect diet and tree-hole nesting is a typical dacelonine. Its most notable characteristic is the startling degree of sexual dichromatism; females are white below and cryptically banded above with black and tawny (and look remarkably like the Neotropical Barred Puffbird, *Bucco radiatus*), while males are buffy below and banded blue on black above. Dimorphism in the tail particularly recalls *Dacelo gaudichaud*, and the banded back and blue-crowned black head of the Bornean race *L. p. melanops* recalls *Melidora*, itself a probable relative of *Dacelo*. Males of more distant races of *Lacedo*, in Sumatra and peninsular Malaysia, are less like *Melidora*, having violet-crowned heads.

Figure 6. Weights of 50 species of kingfishers. The scale is logarithmic and the species are arranged systematically and to some extent geographically to emphasize the range in weights among sympatric congeners. Vertical lines show specific weight ranges (adults); heavy crossbars are averages with the sample size shown; light crossbars are individual weights. Symmetric bars are unsexed individuals or samples; bars to the left of the specific weight-range line are males and those to the right are females. Separate male and female weight-range lines are drawn for those species in which the sexes evidently differ significantly in adult weight. Overall specific means and standard deviations are not shown, since for many species data have been drawn from different populations at different seasons.

Genus *Halcyon* (part, Figure 8)

The White-rumped Kingfisher *(H. fulgida)* is a striking dark-blue and white bird with black head and red bill. It dwells in wooded and forested lowlands of Lombok, Sumbawa, and Flores. It has no obvious close allies. Its color and pattern are quite like the blue-and-white species of *Tanysiptera* and even resemble faintly the distant *Actenoides bougainvillei; fulgida* may prove to have greater affinity with those genera than with *Halcyon*. It is not closely related with the other halcyons, and is included here for convenience only.

The Ruddy Kingfisher *(H. coromanda)* ranges widely on streams in heavy evergreen jungle, nipah palm groves, mangroves, and similar wooded waterside habitats. From Java it extends north to Hokkaido, much farther than any other dacelonine. The more northern birds of the Palaearctic winter in Malesia. It has no obvious close relatives in the genus, although its distinctive violet-washed rufous plumage with blue-white rump and coral bill resembles *H. amauroptera*. The races vary but little, and its range may be discontinuous [*52*]. Its diet includes insects, crustaceans, lizards, fish, and offal. Rand [*81*] provided strong circumstantial evidence that it regularly eats large land-snails in the Philippines, smashing them open on regularly-used "anvil" stones on the forest floor.

I merge with *Halcyon* the three large stork-billed kingfishers. Although usually placed in the genus *Pelargopsis*, they are biologically similar to typical halcyons and differ morphologically only in size and in trivial characters that are probably size-related [*69*]. Even including the storkbills, the genus *Halcyon* embraces a lesser range in the size of its species than does *Chloroceryle*, for instance.

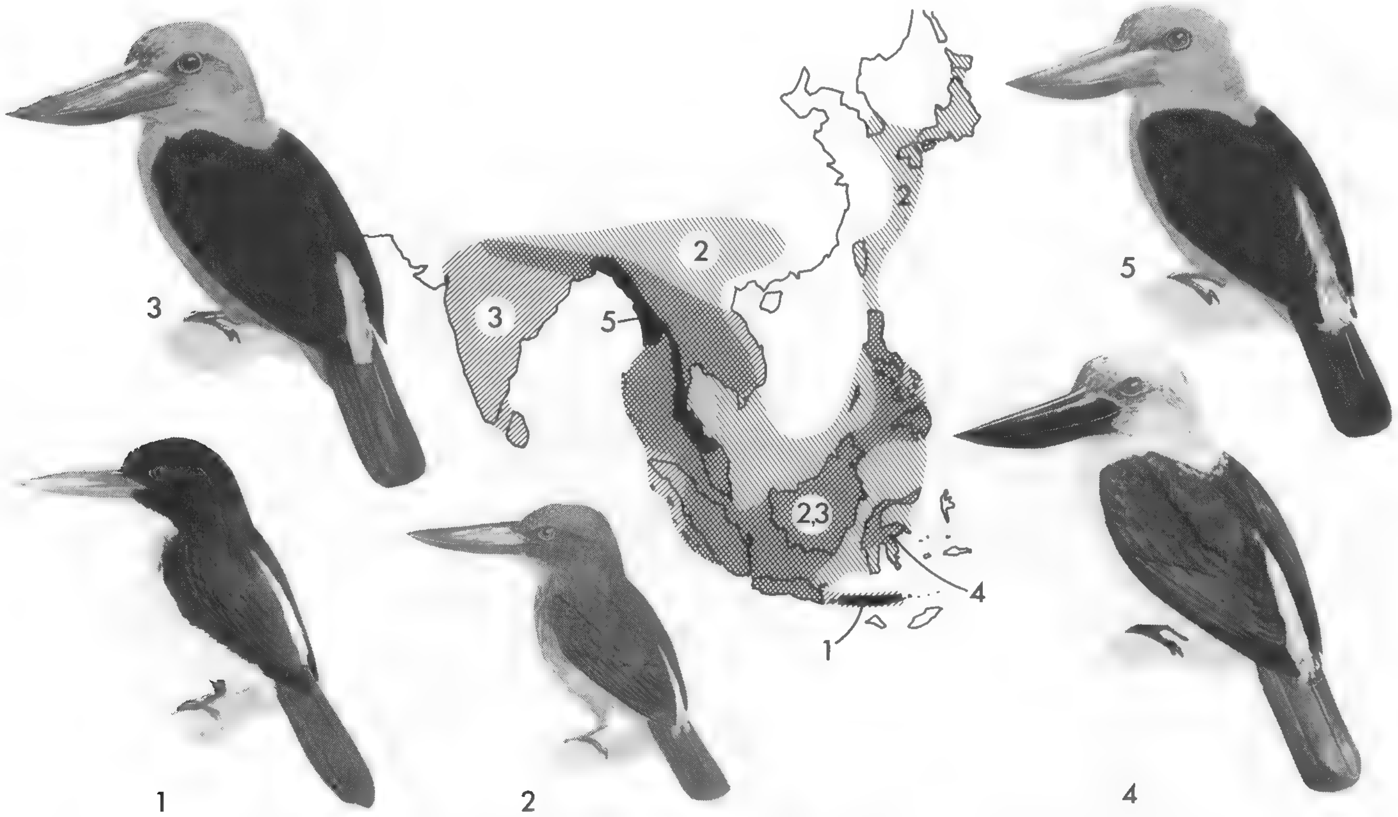


Figure 8. Distribution of five species of the genus *Halcyon*. **1**, *H. fulgida*, White-rumped Kingfisher *(2)*; **2**, *H. coromanda*, Ruddy Kingfisher *(10)*; **3**, *H. capensis*, Stork-billed Kingfisher *(15)*; **4**, *H. melanorhyncha*, Celebes Stork-billed Kingfisher *(3)*; **5**, *H. amauroptera*, Brown-winged Kingfisher *(monotypic)*. Species **3** and **4**, and probably **5** comprise a superspecies.

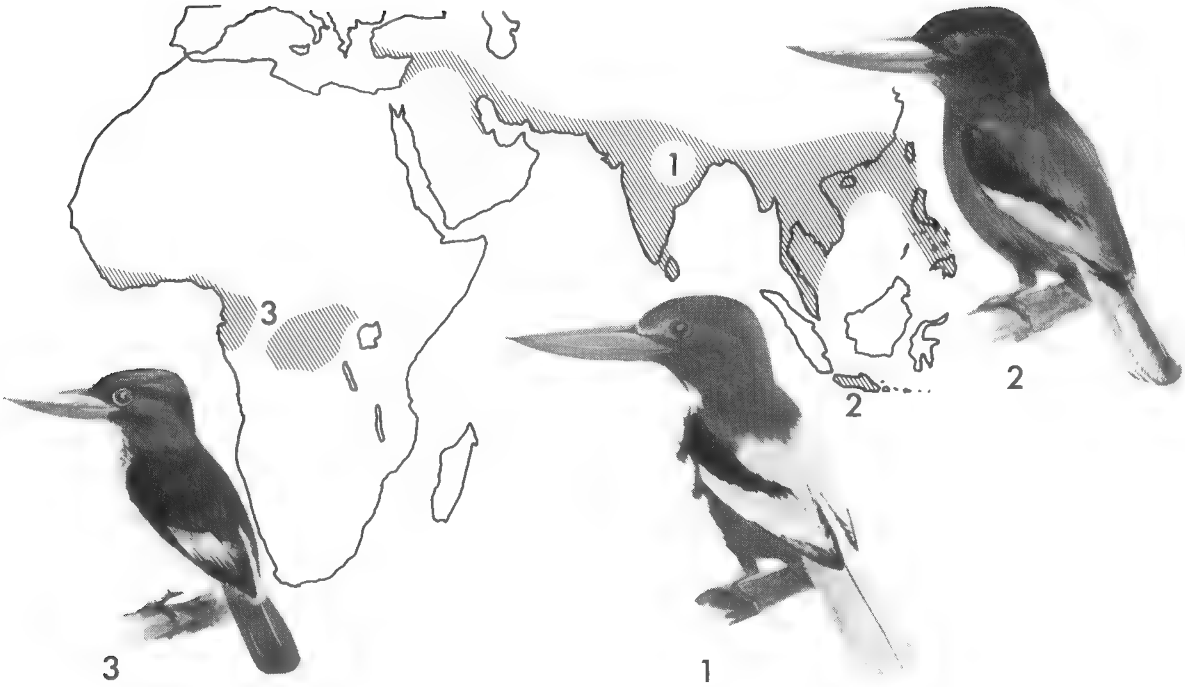


Figure 9. Distribution of three species of the genus *Halcyon*. **1**, *H. smyrnensis*, White-breasted Kingfisher *(5)*; **2**, *H. cyanoventris*, Java Kingfisher *(monotypic)*; **3**, *H. badia*, Chocolate-backed Kingfisher *(3)*. Species **1** and **2** constitute a superspecies.

Stork-billed Kingfishers (Figure 8)

The three species of stork-billed kingfishers are shy birds that live solitarily or in pairs in lowland waterside habitats: forested banks of rivers, swamp forest, estuaries, and mangroves. Brown-winged Kingfishers *(H. amauroptera)* are very much coastal birds, and the slightly larger and much more widespread Stork-bill *(H. capensis)* tends to range also into drier and more open habitats like wooded beaches, hillsides, and paddyfields. *H. melanorhyncha*, endemic to Sulawesi and its offshore islands, is a well-marked allospecies of the last and has much the same habits. Vocal but rather sluggish, stork-bills are fishers, sitting in a tree overhanging water and plunging at a steep angle. If they make a catch, they return to the perch to beat the fish against it, or fly with a stately, non-undulating flight, to a new perch. Henry [*45*] asserts that the diet is mainly fish, but the species also takes crabs, crayfish, frogs, lizards, and a wide variety of insects. Nesting is in rotten tree-holes and reportedly also in earthen banks and termitaria.

H. capensis is rufous, with blue back, rump, wings, and tail and scarlet bill; the sympatric *H. amauroptera* is the same except that back, wings, and tail are brown. *H. melanorhyncha* is cream not rufous, and otherwise a muddy-looking bird with a black bill, but some races have scarlet in the bill and sky-blue in the rump, betraying close affinity with *H. capensis* (C. M. N. White, in prep.).

Genus *Halcyon* (part, Figures 9, 10, 11)

I have discussed elsewhere the interesting systematics of these three Asiatic and seven African "patterned-winged" halcyons in relation to their geography [*36*], and at greater length in relation to new biochemical taxonomic criteria [*37*]. Within the large genus *Halcyon*, these ten kingfishers comprise a natural assemblage of closely-related species. The third

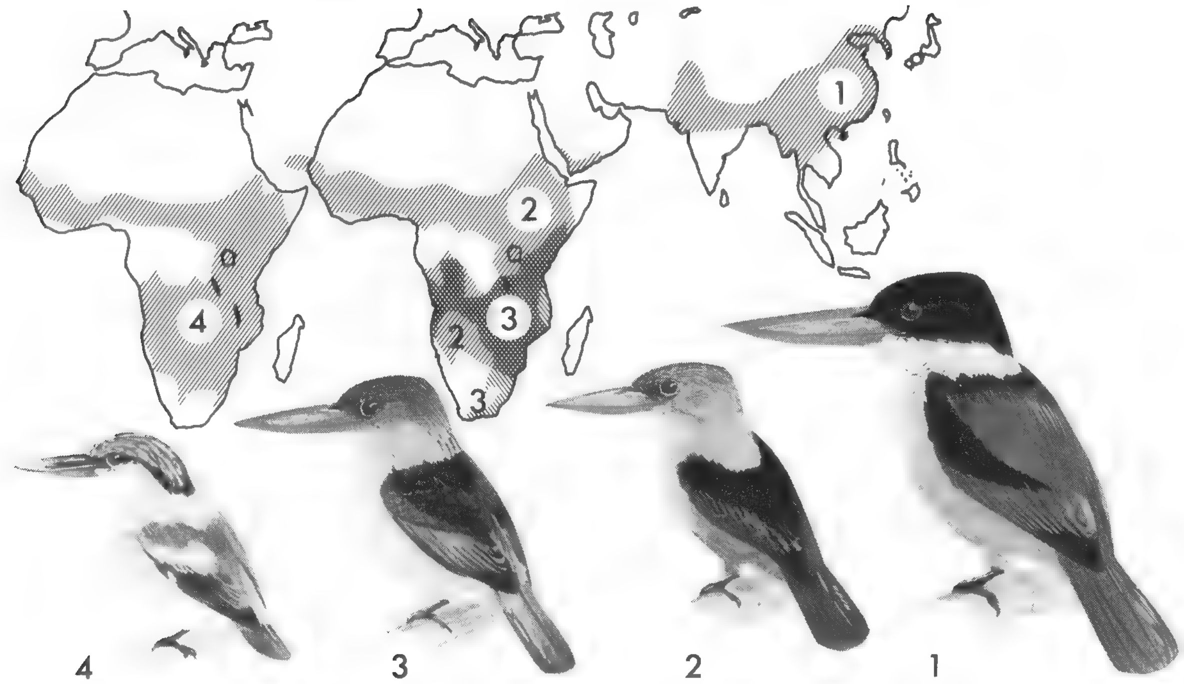


Figure 10. Distribution of four species of the genus *Halcyon*. **1**, *H. pileata*, Black-capped Kingfisher *(monotypic)*; **2**, *H. leucocephala*, Gray-headed Kingfisher *(6)*; **3**, *H. albiventris*, Brown-headed Kingfisher *(3)*; **4**, *H. chelicuti*, Striped Kingfisher *(3)*. Species **1** and **2** constitute a superspecies.

group (Figure 11) is purely African, but the first and the second (Figures 9 and 10) each have African and Asiatic representatives and their ancestors must have ranged repeatedly between the Oriental and Afrotropical regions.

Although its black cap makes the Oriental *H. pileata* look very different from the African *H. leucocephala* (which is only half its weight; see Figure 6), there are underlying plumage resemblances besides the strikingly patterned wings. They have the same waterside and migratory propensities, and their feather proteins are very similar [*56*]. In effect, they comprise a single superspecies ranging from the Cape Verde Islands to Korea, to which the southern African Brown-headed Kingfisher *(H. albiventris)* is closely allied. Africa's Striped Kingfisher, *H. chelicuti* (Figure 12), seems to have its nearest ally in this group, rather than in the first or third groups or among any other *Halcyon* species [*37*]. It is an inhabitant of lightly wooded savannas and penetrates into more arid habitats than does any halcyon other than the Red-backed Kingfisher *(H. pyrrhopygia)* in Australia; the two species look quite alike, but that is probably the result of convergence, since other characters like territorial behavior and feather protein structure are totally dissimilar [*37, 56*].

Preferred habitats of these ten birds vary from sparse woodland (*H. chelicuti*, Figure 13) to rainforest *(H. badia)* and mangroves *(H. senegaloides)*, with most species inhabiting a variety of intermediate wooded situations, including farmland and gardens up to 1,900 meters. The Striped and Brown-headed Kingfishers seem to be entirely independent of water. Breeding territories of Woodland Kingfishers are often near water, although they feed mainly on grasshoppers and rarely fish [*39, 41*]. The most aquatic species, the Black-capped Kingfisher, inhabits forested lakes and rivers, mangroves, and paddyfields.

Most kingfishers of this group are rather strongly migratory, shifting several hundred kilometers but not obviously changing their habitats. In

Nigeria the Gray-headed Kingfisher, like a great many savanna birds, migrates in relation to the annual oscillations of the rain-bearing intertropical front, northward about March to May and south again about September to October. However, since it nests in spring at latitudes between its summer or wet-season range and its winter or dry-season one, its northward migration has to be accomplished in two stages, one pre-breeding and a second post-breeding [*33*].

Striped Kingfishers nest almost exclusively in tree holes and Black-capped Kingfishers in earth banks; the others generally favor one, but use both situations, as well as arboreal termitaria, holes in mud walls of houses, and even swallows' mud nests [*10*]. All species are strongly territorial and maintain their territories by the frequent repetition of a far-carrying call rendered from a tree or telephone wire. Typically, the territorial call consists of a loud initial note followed, after a pause, by a series of evenly spaced notes at the same or falling pitch. The call is clearly homologous among the African species at least [*13*] but varies specifically in duration, pitch, number, and frequency of notes, to give either an easily imitated series of measured, strident whistles *(H. badia, H. malimbica)*, or a fast whinnying rattle lasting for three seconds *(H. smyrnensis, H. senegalensis, H. albiventris)*, or a *cheer-oh* call in the case of *H. chelicuti*, in which the 15 to 20 notes of the *oh*, all delivered in one-half second, cannot be separately discerned by the human ear at any distance (see sonagrams in Greig-Smith [*39, 40*]). It provides a particularly good example of the adaptation of voice structure to

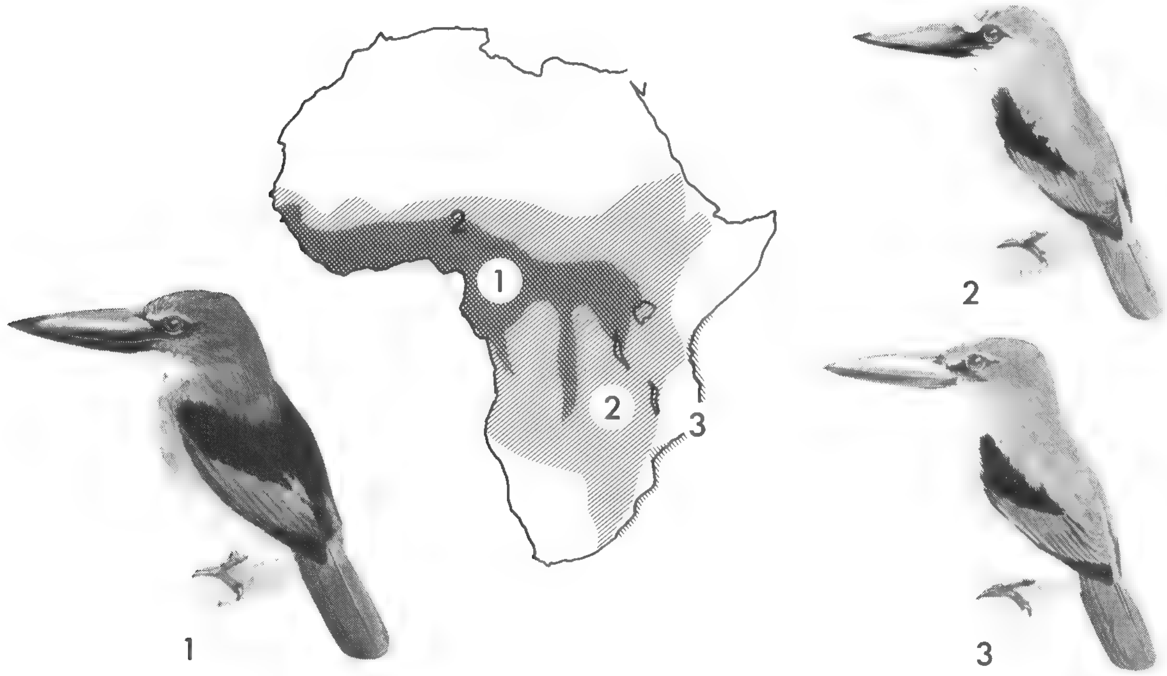


Figure 11. Distribution of three species of *Halcyon*. **1**, *H. malimbica*, Blue-breasted Kingfisher *(6)*; **2**, *H. senegalensis*, Woodland Kingfisher *(3)*; **3**, *H. senegaloides*, African Mangrove Kingfisher *(2)*. Species **2** and **3** constitute a superspecies.

TABLE 1

The Diet of White-breasted Kingfishers
Halcyon smyrnensis in the Sundarban, India*

Type of Food	*Items*		*Weight (percent)*		
	Number	*Percent*	*Wet season*	*Dry season*	*All year*
Earthworms	13	1.5	2.1	1.0	1.5
Decapod crustaceans	124	14.3	10.0	12.5	11.2
Insects	235	27.1	11.1	21.2	16.2
Fish	184	21.2	43.0	19.4	31.2
Frogs, toads	235	27.2	25.0	13.1	19.1
Lizards	31	3.6	8.8	18.7	13.9
Snakes	24	2.8			
Mice	12	1.4	0	14.1	6.9
Squirrels	7	0.9			
Totals	865	100.0	100.0	100.0	100.0

*Data from Mukherjee (1973).

the environment [*12, 13*]; *Halcyon* species of open habitats have short, shrill, modulated notes rich in harmonics while those in forests have long, pure, falling notes which, at the cost of their information content, effectively penetrate that habitat.

At least seven of these species, and probably all ten, often accompany the territorial call with a highly conspicuous postural display. The bird perches very erect, with the tail cocked and fanned, and flicks the wings open to show the bold ventral pattern of black, chestnut, and white (figured in Fry [*37*]). The Woodland Kingfisher pivots rapidly from side to side, while holding the wings fully outstretched and vibrating for a few seconds; the Striped Kingfisher repeatedly spreads and closes the wings [*39, 40*]. Displays are most intense in a social context. Some observers have interpreted them as having a courtship function, but Greig-Smith [*40*] thought that, with the song, they function more importantly in territorial proclamation. Mates, perched adjacently, often direct the wing-spreading display at each other and call together. Duetting is particularly conspicuous in the Striped Kingfisher, and Wickler [*108*] interpreted it as a communal territorial display. Reyer [*83*] found that 20 percent of territories are occupied and defended by three birds each, the mated pair and a helper. He also described sexual dimorphism in the underwing pattern. The Gray-headed Kingfisher also has an antiphonal song [*13*].

Grasshoppers feature importantly in the diets of African dry-land halcyons, and the Striped Kingfisher carries them to its young, much as *Alcedo* kingfishers carry small fish, held in the bill head-first. Larger halcyons catch termites on the wing, pluck skinks from tree-trunks, dive into shallow water for shrimp, crabs, and fish, and take munias *(Lonchura)*, mice, and nestling birds [*15, 70*]; but arthropods captured in a swoop to the ground are the main prey, and include scorpions *(Uroplectes, Isometrus)*, millipedes *(Julus)*, centipedes *(Scolopendra)*, and a large variety of insects. One of the most detailed dietary analyses for any kingfisher was made by Mukherjee [*74*] with the White-breasted Kingfisher in the West Bengal Sundarban, and his findings are summarized in Table 1. G. Robertson (pers. commun.) watched

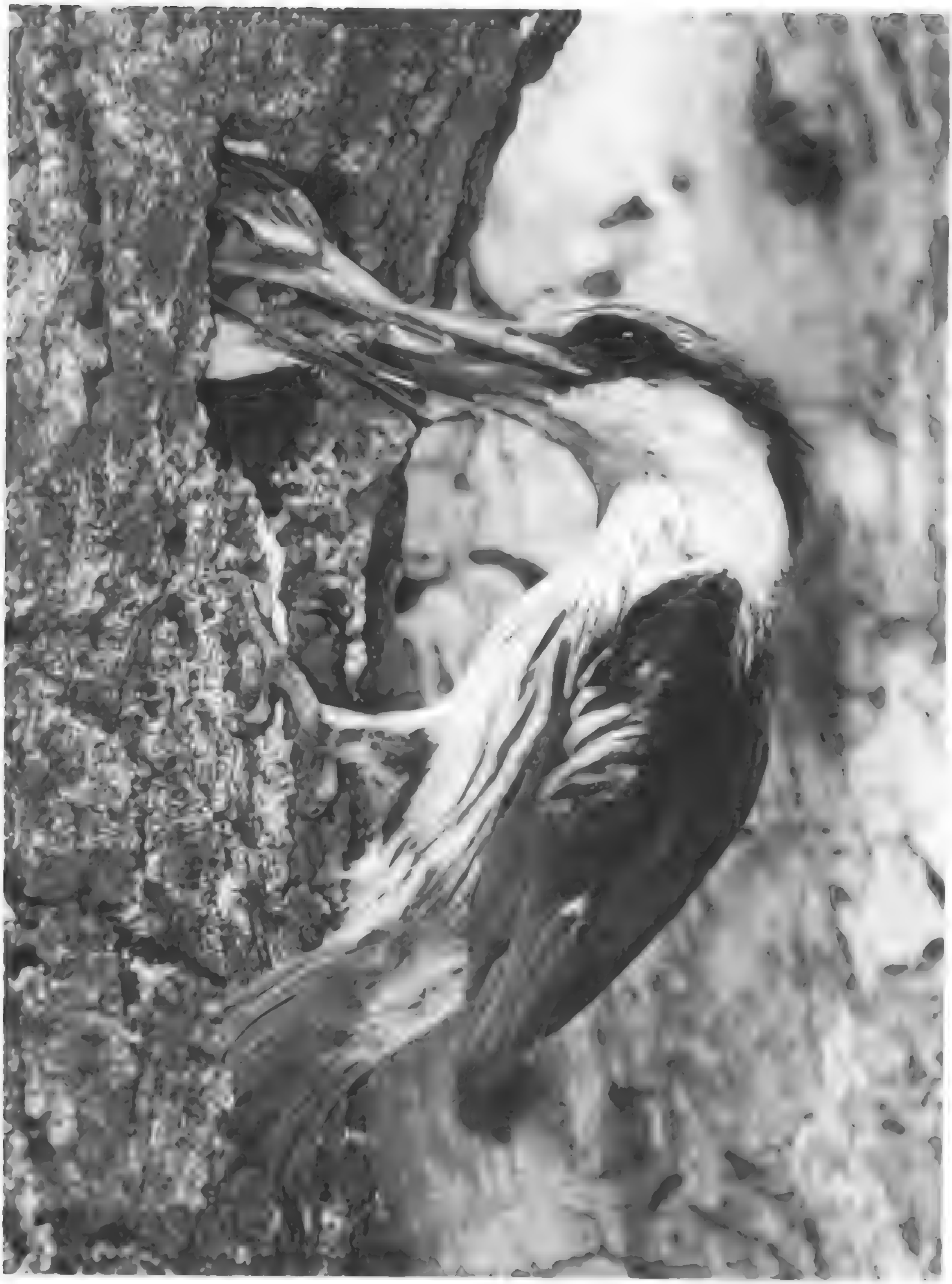


Figure 12. Striped Kingfishers, *Halcyon chelicuti*, Rhodesia. Photograph by Peter Steyn.

this species forage on arable ground by upturning earth with its bill and searching out invertebrates, evidently with much success.

Genus *Halcyon* (part, Figure 14)

The last six of these eight, mainly blue-and-white halcyons are small tree kingfishers (Figure 14) that range allopatrically from the Moluccas to the New Hebrides and clearly comprise a superspecies. They bear little plumage resemblance with the previous groups of Asiatic and African *Halcyon* species, but are quite closely allied with the next assemblage of 12 halcyons (Figure 15), although demarcated from them by the extent and nature of sexual plumage dimorphism. Figure 14 shows females of this *H. macleayii* superspecies. Males differ from females in having white underparts, collars, or backs; but in the Chestnut-bellied Kingfisher both sexes have the lower underparts chestnut and only the female has a white vent. Within the superspecies, the Forest (southern New Guinea, north and east Australia), Blue-and-white (Moluccas: Morotai to Obi), Lazuli (Moluccas: Ceram, Ambon, Haruku) and New Britain (New Britain) Kingfishers are so closely related that they might justifiably be treated as a single polytypic species. In fact *H. lazuli* is usually treated as a race of *H. diops*; here I separate them because *H. diops* more closely resembles *H. macleayii* than *H. lazuli*.

The Blue-black Kingfisher is a larger bird, parapatric or narrowly sympatric with *H. macleayii*. The male has blue-and-white underparts in two subspecies, *H. n. nigrocyanea* (Figure 14) and *H. n. stictolaema*, and chestnut and white in *H. n. quadricolor*; the females are all white-bellied. Juvenile females of *H. nigrocyanea* and of *H. diops* are alike in having brown pectoral bands. *H. nigrocyanea* seems to be rather more closely related to the *H. macleayii* superspecies than to the even larger Winchell's Kingfisher *(H. winchelli)* of the southern Philippine islands, in which the sexes are alike except for the females having buffy underparts. In all eight species of this group, juveniles are brownish, being most pronounced in *H. winchelli*.

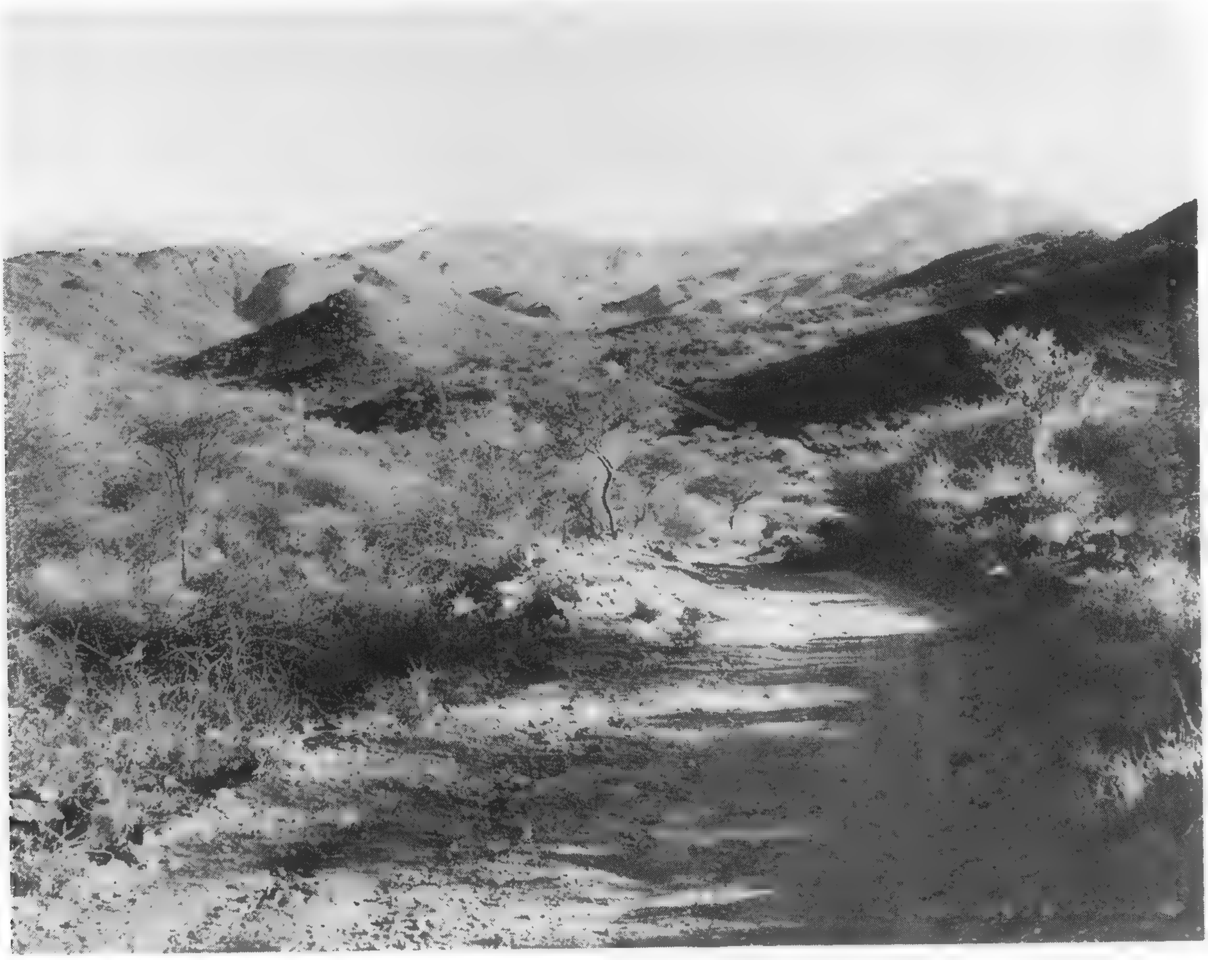


Figure 13. *Acacia* savanna, Samburuland, northern Kenya. Habitat of the African Pygmy Kingfisher *(Ceyx pictus)*, the Striped Kingfisher *(Halcyon chelicuti)*, and others.

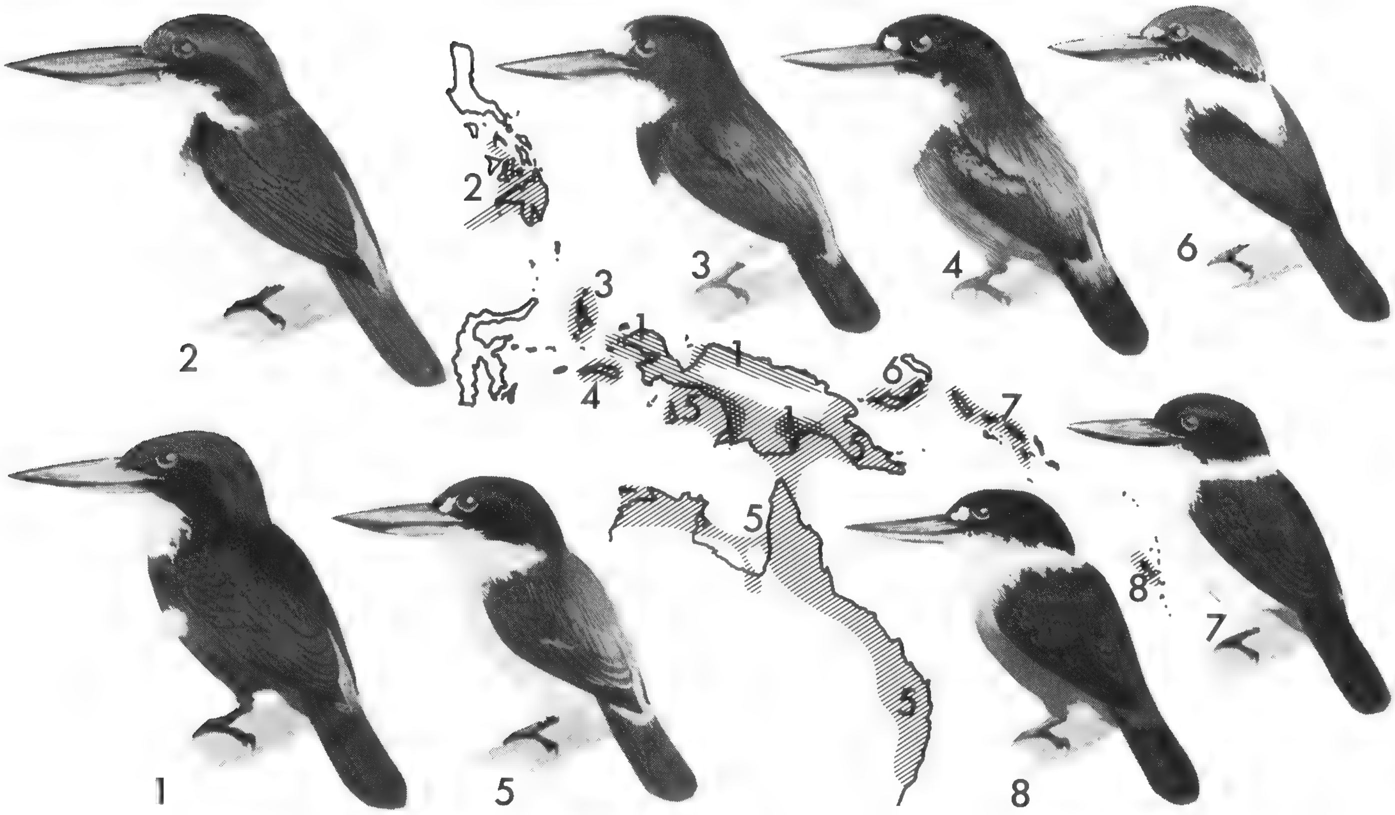
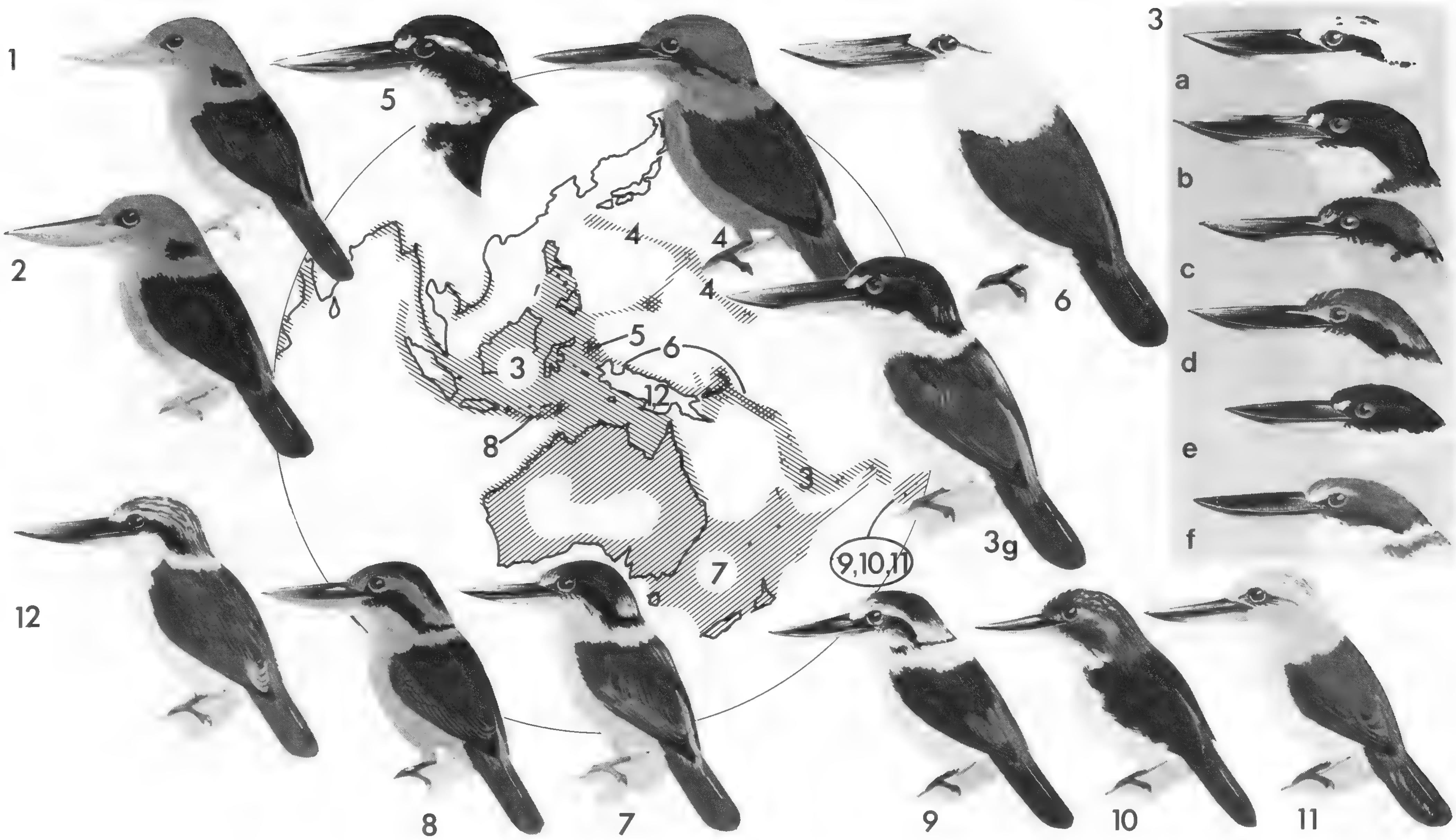


Figure 14. Distribution of eight species of the genus *Halcyon*. **1**, *H. nigrocyanea*, Blue-black Kingfisher, ♂ *(3)*; **2**, *H. winchelli*, Winchell's Kingfisher, ♂ *(2)*; **3**, *H. diops*, Blue-and-white Kingfisher, ♀ *(monotypic)*; **4**, *H. lazuli*, Lazuli Kingfisher, ♀ *(monotypic)*; **5**, *H. macleayii*, Forest Kingfisher, ♀ *(3)*; **6**, *H. albonotata*, New Britain Kingfisher, ♀ *(monotypic)*; **7**, *H. leucopygia*, Ultramarine Kingfisher, ♀ *(monotypic)*; **8**, *H. farquheri*, Chestnut-bellied Kingfisher, ♀ *(monotypic)*. Species **3** through **8** constitute a superspecies.

In the Philippines, Moluccas, New Guinea, and Australia the species inhabit swampy forest, forested streams, mangroves, and dense woodland, while those in the Bismarck Archipelago, New Britain, and New Hebrides are birds of true forest. Specific forest habitats depend in part on congeneric competition. The Chestnut-bellied Kingfisher, which is endemic to the northwestern New Hebridean islands of Espiritu Santo, Aore, Malo, and Malekula, inhabits primary forest and excludes the same-sized Mangrove Kingfisher *(H. chloris)*, which strictly inhabits adjacent open areas. On southern islands 120 km away, where the Chestnut-bellied Kingfisher is absent, the Mangrove Kingfisher lives in all habitats from open shore to closed forest [*67*]. *H. farquheri* inhabits the understorey as well as the canopy; but its allospecies *H. albonotata* in New Britain is confined to the canopy by competition with the similar-sized *Tanysiptera sylvia*, which occupies the understorey [*26*]. On Bougainville Island in the Solomons the Ultramarine Kingfisher *(H. leucopygia)* is also a canopy bird, possibly excluded from the understorey by the larger *H. chloris* and the much larger *Actenoides bougainvillei* [*23*].

Species of this *Halcyon* assemblage nest in tree-holes and arboreal termitaria (G. Robertson, pers. commun., found 13 nests of *H. farquheri* in holes in tree-ferns and 24 in termitaria) and feed on crabs, fish, lizards *(H. nigrocyanea)*, caterpillars, grasshoppers, centipedes, spiders, and frogs *(H. macleayii)*. The Chestnut-bellied Kingfisher is entirely insectivorous, and catches small moths and beetles in flight. It also forages on the ground, probing into forest litter and upturning soil in search of insects (G. Robertson, pers. commun.). The Forest Kingfisher is sedentary in New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Guinea and northern Australia, but the population breeding from southern Queensland to south of the Macleay River in New South Wales is migratory, and winters from the eastern Lesser Sunda Islands to New Britain. In "winter," immigrants outnumber resident birds in New Guinea and are territorial, a pair returning to the same winter territory in successive years (H. L. Bell, pers. commun.).

Halcyon farquheri, the most distant from New Guinea of the blue-and-white halcyons, has several characters allying it with the following group of green-and-white species. Like some of them it is a flat-billed flycatcher. Its voice is like that of *H. chloris* (G. Robertson, pers. commun.), which can also be black-capped (Figure 15). The marked tendency of green-and-white halcyons to evolve buff and cinnamon plumages could account for the rufous belly of *H. farquheri.*

Genus *Halcyon* (part, Figure 15)

This large assemblage is mapped together (Figure 15) because the parapatric distributions (i.e., distributions which are in geographical contact but do not overlap) of most of the species suggest they are closely related. They also share similar plumages: sea-green upperparts, and white or buff collars and underparts. Specific sizes vary considerably. Specimens of some weigh only a little over 30 grams *(H. torotoro, H. sancta),* others four times as much (*H. saurophaga,* Figure 6). Preferred habitats vary from forest and woodland to shores and atolls, and diets embrace a range of invertebrates and vertebrates taken on dry land or from water, according to the habitat of each species. Sacred Kingfishers *(H. sancta)* can take insects in flight, and all of the Polynesian species *(H. tuta, H. venerata,* and *H. gambieri*) feed like flycatchers, actively making sallies from a perch to seize insect prey in foliage, from trunks, branches, the ground, and water, occasionally also snatching them in flight [*47, 51*]. Most species nest exclusively in tree holes and arboreal termitaria, but in Australia, Red-backed Kingfishers generally nest in tunnels which they excavate in the vertical banks of wet or dry creeks. In New Zealand, Sacred Kingfishers (arboreal in Australia) often nest in man-made banks and road-cuttings. Mostly, the species of this group are sedentary; however, southern Australian Sacred Kingfishers (but evidently not New Zealand ones) migrate north nearly to the Equator after breeding.

Yellow-billed Kingfishers (Figure 15)

In this subgroup, *H. torotoro* inhabits lowland New Guinea and south to 14° S Lat. in the Cape York Peninsula, and *H. megarhyncha* is its montane

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Figure 15. Twelve species of the genus *Halcyon*. Distributions of species **1** and **2** (New Guinea, throughout) and species **12** (Australia, throughout) are not shown. **1**, *H. torotoro,* Yellow-billed Kingfisher *(7)*; **2**, *H. megarhyncha,* Mountain Yellow-billed Kingfisher *(3)*; **3**, *H. chloris,* Mangrove Kingfisher *(47,* includes *H. enigma)*; **4**, *H. cinnamomina,* Micronesian Kingfisher *(3,* includes *H. miyakoensis)*; **5**, *H. funebris,* Somber Kingfisher *(monotypic)*; **6**, *H. saurophaga,* Beach Kingfisher *(3)*; **7**, *H. sancta,* Sacred Kingfisher *(9,* includes *H. recurvirostris)*; **8**, *H. australasia,* Lesser Sundas Kingfisher *(5)*; **9**, *H. tuta,* Pacific Kingfisher *(5,* includes *H. ruficollaris* and *H. godeffroyi*; vernacular name is new); **10**, *H. venerata,* Tahiti Kingfisher *(2)*; **11**, *H. gambieri,* Tuamotu Kingfisher *(monotypic)*; **12**, *H. pyrrhopygia,* Red-backed Kingfisher *(2)*. The following races of *H. chloris* are illustrated: **3a**, *matthiae*; **3b**, *sordida*; **3c**, *tristrami*; **3d**, *juliae*; **3e**, *colona*; **3f**, *armstrongi*; **3g**, *collaris*. For the distributions of species **9**, **10**, and **11** within hatched area of the Pacific, see text. Species **1** and **2** constitute a superspecies; species **7** through **11** constitute another superspecies.

counterpart. The two are sometimes placed in their own genus *(Syma)* on the basis of saw-edged bills. *H. torotoro* has irregular small "teeth" on the distal half of the maxilla only. *H. megarhyncha*, which weighs 50 percent more than the lowland species and has a bill 20 percent longer, has larger and more regular "teeth" distally on the maxilla and, in some specimens, minute regular ones on the mandible. In all other respects these birds are so like the remaining kingfishers in the group (subgenus *Todiramphus*, with the *Halcyon macleayii* group of species) that generic separation is unwarranted. Both yellow-billed kingfishers are true forest birds and are altitudinal allospecies, completely segregated at about 1,000 meters. From there *H. torotoro* ranges down to sea level and *H. megarhyncha* up to 2,150 meters; in the Karimui basin the highest record of the former was 1,120 meters and the lowest of the latter 1,340 meters [*22*]. In both species immatures have black bills and adult females have a large black patch in the center of the crown (Figure 15 shows males). The diets include earthworms, lizards, and dragonflies. Both species are notable for their calls, presumably territorial songs: a loud "police whistle" trill of two to seven seconds duration, rising and falling in pitch.

Mangrove Kingfisher and Allies (Figure 15)

This group of halcyons is dominated by the Mangrove Kingfisher *(Halcyon chloris)* by virtue of its huge geographical range and its many races. It is distributed along tropical sea-shores (Figure 16) from the Red Sea to the eastern Samoan Islands (Tutuila, Ofu, Olosinga, Tau), a distance of 16,000 km. These kingfishers inhabit mangroves, tree-lined beaches, estuaries, tidal forest, and also gardens, cultivated fields, and lightly wooded country as high as 1,700 meters above sea level. About 50 subspecies have been described, and some of the more readily defined ones are illustrated in Figure 15. Most are colored aquamarine or ultramarine and white, but some are dark olive and several have the white parts more or less strongly suffused with buff, such as *H. c. tristrami* of New Britain and *H. c. juliae* of the central New Hebrides (Figure 15). T. H. Harrisson (unpubl., but see Smythies, [*97*]) studied the breeding biology of the Mangrove Kingfisher in Borneo. A pair bored up to eight holes in a tree-trunk, finishing two or three, and reared two broods in quick succession from different holes. During the nestling period of 44 days, lizards were the main food fed to nestlings. Other prey items, in decreasing importance, included the scarab beetle *Exophilis hypoleuca*, tree frogs, carpenter bees taken on the wing, grasshoppers, small snakes, and earthworms taken off or out of the ground.

The Micronesian Kingfisher *(H. cinnamomina)* might be regarded merely as a race of *H. chloris*, from which it differs mainly in being rufous-headed, if the two birds were not sympatric on Palau Island. Here *H. cinnamomina* inhabits secondary forest while *H. chloris* occupies coconut groves and beaches; moreover, *H. cinnamomina* has rufous, not white, underparts, although its other races on the Caroline Islands and on Guam are white below. The Miyako Kingfisher *(H. miyakoensis)* [*105*], known only from the unique type taken in 1887 in the Ryukyu Islands, was probably a race of *H. cinnamomina* [*66*].

The Somber Kingfisher *(H. funebris)* is endemic to Halmahera Island in the Moluccas, where it occurs in the lowlands; further field information is lacking. It resembles the dark *Halcyon chloris sordida* of southern coastal New Guinea (C. M. N. White, in prep.) and also the white-collared race *(H. chloris colona)* on islands southeast of New Guinea; *H. funebris* is treated as

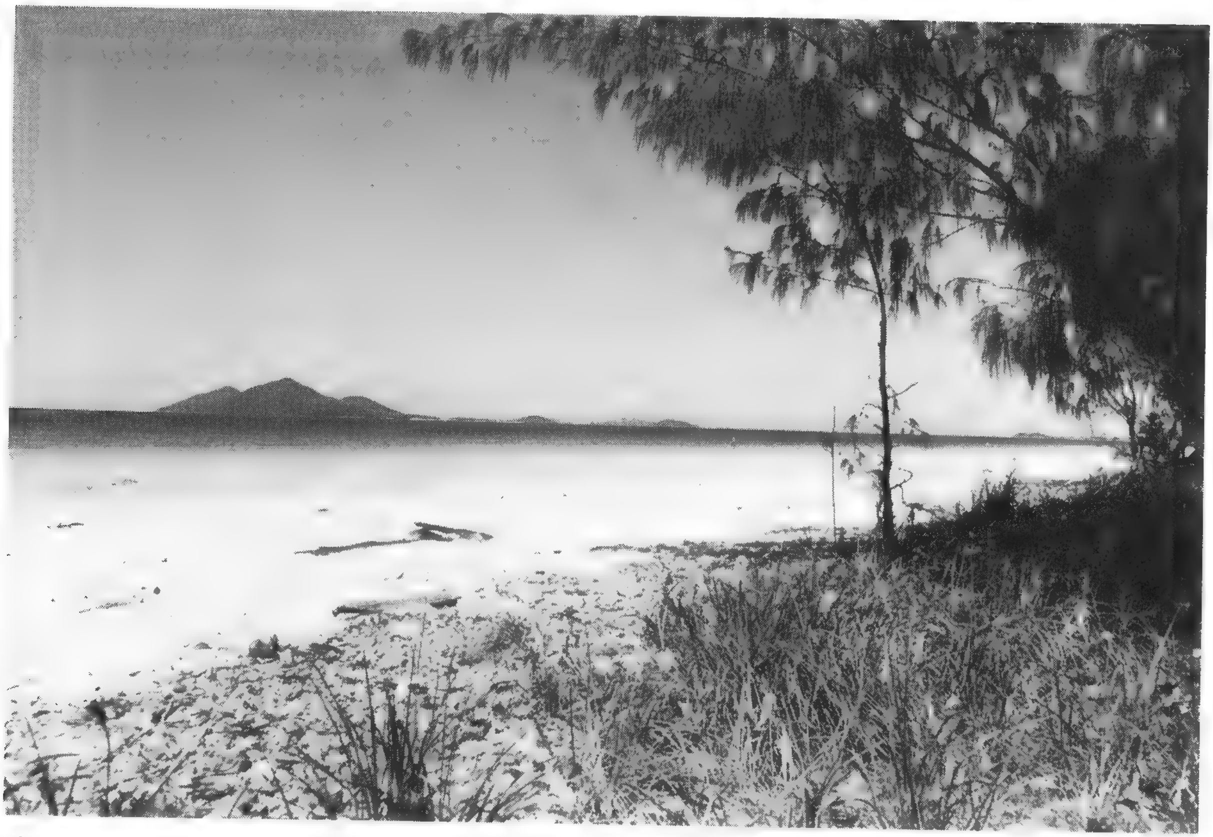


Figure 16. Tropical beach habitat of the Mangrove Kingfisher *(Halcyon chloris)*, mouth of the Johnstone River, northern Queensland, Australia.

specifically distinct from *H. chloris* since a population of the latter also occurs on Halmahera and remains reproductively isolated from *H. funebris*.

Another near relative of *H. chloris*, partly sympatric with it but with very similar plumage, is the Beach Kingfisher *(H. saurophaga)*. It prefers the more restricted coastal habitats, especially coral cliffs, coconut groves, and mangroves from the Moluccas along the northern New Guinea coast to the Solomons, and it feeds on crabs, insects, fish, and lizards [*65*, *82*]. In the Solomon Islands it hovers and plunge-dives for fish, sometimes hunting 100 meters offshore (E. C. Fellowes, pers. commun.). Competition with *H. chloris*, where the two species are sympatric, is probably reduced or avoided by differences in size, *H. saurophaga* being about twice as large (Figure 6). Green-capped examples of Beach Kingfishers sometimes occur and, since both green- and white-capped nestlings have been found in the same brood, the variation is probably polymorphic rather than age- or sex-related [*66*]. In the Admiralty Islands eight percent of the population is green-capped with an additional 32 percent having some green crown feathers, while half the population in the nearby Hermit and Ninigo Islands, and all of it on Anchorite Island, are green-capped ([*66*]; n=60). In the Saint Matthias Islands, between the Admiralty Islands and the Bismarcks, Mangrove Kingfishers *(H. c. matthiae)* have white heads with some black crown feathers (Figure 15) and look like *H. saurophaga*. In other features they resemble *H. cinnamomina*, and Mayr [*66*] speculated that the latter may have originated from ancestral *H. chloris matthiae*.

Another unresolved taxonomic problem concerns the Mangrove Kingfishers of Talaut Islands between Halmahera and Mindanao. On Karkellung Island in this group there occur two exclusive size ranges. The larger ones, typical *H. chloris*, appear to be resident but have not yet been proved to breed there. If breeding becomes proven, the smaller birds, which are breeding residents, would have to be specifically separated as *Halcyon enigma* (C. M. N. White, in prep.). In the meantime Eck [*32*] has argued that they should be treated as conspecific

Sacred Kingfisher and Allies (Figure 15)

To the south of *H. chloris* and parapatric with it, is found the widespread and well-known Sacred Kingfisher *(H. sancta)*, whose nine races extend from western Australia and southern New Zealand to New Caledonia and the western Samoan Islands (Upolu, Savaii). It is smaller than *H. chloris*, similar in plumage but buffy, never pure white, below, and with much the same habits and habitats: coasts, forest clearings, woods, farmland, and lake shores. Most, but not all, races have rather flat bills. As well as flycatching, Sacred Kingfishers catch fish by flopping onto the surface of the water and also by diving steeply with folded wings, like *Alcedo*. Sacred Kingfishers also eat worms, spiders, crustaceans, tadpoles, lizards, mice, and small birds including ducklings (E. F. Stead, 1932, and G. J. H. Moon, 1957, cited in Falla, Sibson and Turbott [*34*]).

Customarily the flat-billed kingfisher of western Samoa has been treated as a distinct species, *Halcyon recurvirostris*, but its bill is no flatter dorsoventrally than that of *H. sancta macmillani* of the Loyalty Islands; it shares with *H. sancta* the same habits [*21*], and differs quite inconsequentially from *H. sancta* in plumage; so I place it without hesitation as a race of the Sacred Kingfisher.

Another small woodland kingfisher, *H. australasia* of the Lesser Sundas, looks much like *H. sancta* but is rich buff in place of buffy white, with cinnamon collar and eyebrow. I agree with C. M. N. White (in prep.) that it is an allospecies of *H. sancta*, and note that in plumage it differs from typical Sacred Kingfishers in almost exactly the same way that *H. chloris juliae* or male *H. c. cinnamomina* differ from typical Mangrove Kingfishers.

Scattered throughout Polynesia are several more forms of small, sea-green and white or buffy kingfishers and, since they have very flat—almost recurved—bills, they are derived more likely from *H. sancta* than from *H. chloris*. They inhabit secondary forest and plantations on volcanic islands and atolls [*51*], up to 1,700 meters on Tahiti, and are flycatchers and plunge-fishers, also eating lizards and crustaceans [*47, 49*]. They nest in tree holes.

The nominate race of the Pacific Kingfisher (*Halcyon tuta*, Figure 15), from Tahiti and four adjacent Society Isles, resembles in plumage a diminutive Beach Kingfisher of the green-capped form. Two races *(H. t. atiu* and *H. t. mauke)* described from the Cook Islands by Holyoak [*48*], have the light parts not snowy but buffy, thus closely resembling *H. sancta*. A third population, from Mangaia in the Cook Islands, was described by Holyoak [*48*] as a full species, *H. ruficollaris*; its orange-buff head capped with green resembles *H. sancta*, while the rest of the plumage looks like *H. tuta*, demonstrating the close affinity of *ruficollaris* with those two species. Although *ruficollaris* differs biologically from the other Cook Island kingfishers in its voice, the plumage differences are much less than among the races of *H. chloris* or of *H. cinnamomina*, and so I unite it with *H. tuta*. Moreover, the White-crowned Kingfisher of the Marquesas Isles, *H. godeffroyi*, resembles *H. tuta* in plumage, size, and bill shape; it, too, is best treated as a race of that species.

The Tuamotu Kingfisher *(H. gambieri)* now exists only on the tiny island of Niau and numbers 400 to 600 birds [*50*]. The population there *(H. g. gertrudae)* has a buffy white head (Figure 15) like so many other taxa in the *H.*

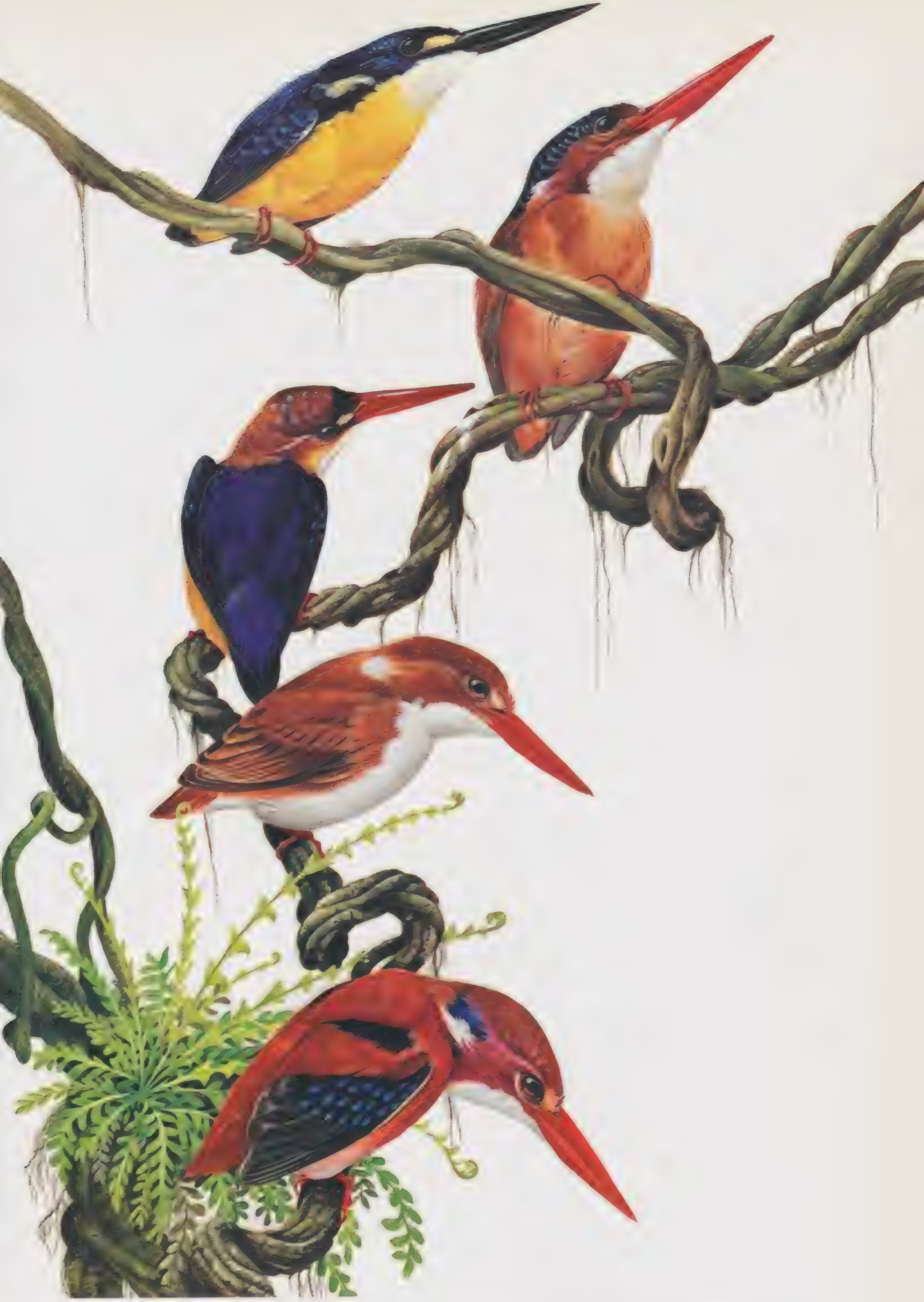


Plate 2. Five species of kingfishers of the genus *Ceyx*. From top to bottom: Variable Dwarf Kingfisher, *C. lepidus solitarius*; Celebes Dwarf Kingfisher, *C. fallax sangirensis*; African Dwarf Kingfisher, *C. lecontei leconti*; Madagascar Pygmy Kingfisher, *C. madagascariensis*; Philippine Dwarf Kingfisher, *C. melanurus samarensis*. Painting by Terence Lambert.

chloris-H. sancta assemblage. The nominate subspecies lived on Mangareva in the Gambier Isles 1,250 km to the southeast, but died out by about 1922 [*50, 101*]. Like nominate *H. tuta* a narrow black line separated the white collar from the buffy crown.

The Tahiti Kingfisher *(H. venerata)* has one population on that island (Figure 15) and another, browner one on adjacent Moorea. Each is widespread, even common, in forest. Tahiti is the only South Pacific island with two species of kingfishers *(H. tuta, H. venerata)*, and it is significant that, of ten island populations measured by Holyoak and Thibault [*51*], the largest was one Tahiti population *(venerata)* and the smallest the other *(tuta)*. In linear measurements *H. tuta* on Tahiti is about 10 percent larger than *H. venerata* there.

Red-backed Kingfishers *(H. pyrrhopygia)* are endemic to Australia, occurring throughout the continent in mallee, mulga, and a variety of savanna habitats. Southern populations are migratory. This species resembles *H. chloris* and *H. sancta* in plumage except for the streaked crown and cinnamon rump; the bill shape resembles *H. chloris*. Its voice differs markedly from both. The diet includes locusts and mice [*46*].

Subfamily Alcedininae

Genus *Ceyx* (part, Figure 17, Plate 2)

Five of the dwarf kingfishers (Plate 2) are allopatric inhabitants of Palaeotropical rainforests; one is found in African savannas but also in the Congo basin where it is broadly sympatric with its forest congener (Figure 7). Mostly they favor the vicinity of water, frequenting forested river banks and small streams and rain-pools deep within the forest. They keep strictly low, flying and perching within two or three meters of the ground and feeding at its surface; they shun open, sunlit places. Nest holes are excavated in low earthen banks, often by streams. The African Pygmy Kingfisher *(C. pictus)* nests in similar places in savanna, including erosion gullies and ground termite mounds. It lives often far from water in arid grassland and scrub country (Figure 13), foraging from low vegetation or from wires.

Small arthropods are the main food of all six species: spiders and a variety of insects, mainly grasshoppers. *C. pictus* also occasionally eats small frogs and fish and aquatic insects, and I have observed the Oriental Dwarf Kingfisher *(C. erithacus)* in Johor, Malaysia and in Sarawak hunting from perches near stagnant puddles in deep forest, diving equally to the forest floor and into water for arthropods and tadpoles. In Sri Lanka this species is said to be largely aquatic in habitat and diet.

The dwarf kingfishers forage by perching silently, intently scanning the ground nearby, bobbing the head and sometimes the tail, and suddenly diving to snap up prey in the tip of the bill. As terrestrial prey is seized, the kingfishers may stand momentarily on the ground, but generally they return directly to the vantage perch to beat the prey before swallowing it whole. Foraging behavior, the low direct flight, and the weak monosyllabic voice are much like *Alcedo* kingfishers. The latter are more specialized than members of the genus *Ceyx* only in the sense that they are considerably more piscivorous.

I have discussed the mutual affinities of these six species in some detail [*37*]. They are rufous birds with scarlet bills and legs, are three- or four-toed, and all except the Madagascar Pygmy Kingfisher *(C. madagascariensis)* have

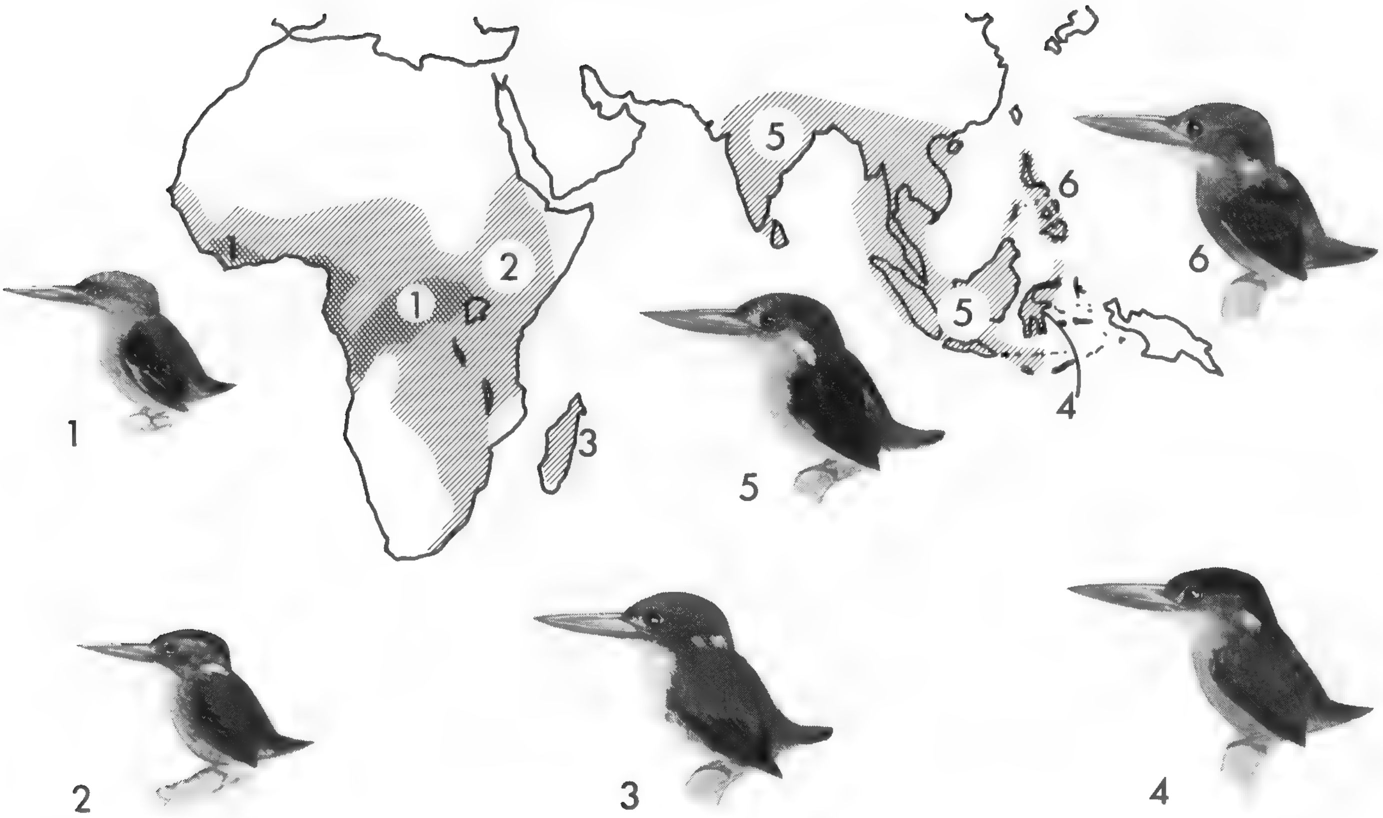


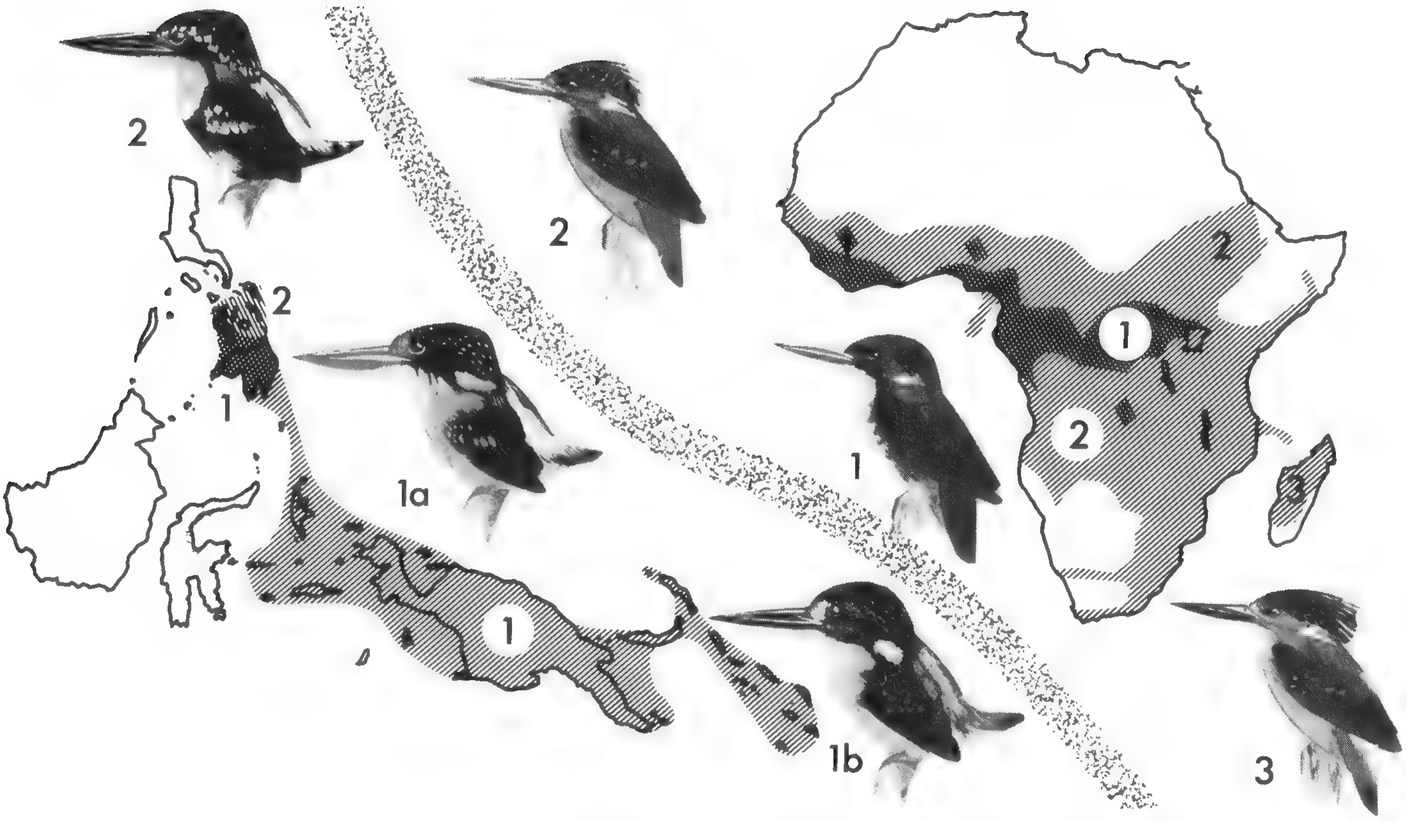
Figure 17. Distributions of six species of the genus *Ceyx*. **1**, *C. lecontei*, African Dwarf Kingfisher *(2)*; **2**, *C. pictus*, African Pygmy Kingfisher *(3)*; **3**, *C. madagascariensis*, Madagascar Pygmy Kingfisher *(monotypic)*; **4**, *C. fallax*, Celebes Dwarf Kingfisher *(2)*; **5**, *C. erithacus*, Oriental Dwarf Kingfisher *(7)*; **6**, *C. melanurus*, Philippine Dwarf Kingfisher *(3)*. For *C. erithacus*, several other vernacular names are used regionally. Species **5** and **6** constitute a superspecies.

some blue plumage dorsally. The two African birds are four-toed and so alike in plumage that they would be treated as a superspecies, were it not that the adult form of the bill differs and their ranges overlap. They are very like the Celebes Dwarf Kingfisher *(C. fallax)*, which has three whole and one vestigial toe, and they also resemble the three-toed *C. erithacus-C. melanurus* superspecies. *Ceyx madagascariensis*, another four-toed bird, is probably genetically closer to the Oriental than to the African dwarf kingfishers, and probably invaded Madagascar directly across the Indian Ocean [*37*].

What I call here the Oriental Dwarf Kingfisher comprises rufous- and black-backed forms often regarded as full species. Two races of rufous-backed forms range from Sumba in the Lesser Sundas to peninsular Thailand and to Mindoro in the Philippines. In the northern part of its range (Mindoro, Malaysia, Sumatra) are found also black-backed dwarf kingfishers, in part breeding residents and in part migrants from the north, where they range polytypically from India to Hainan. Numerous hybrids are known from the zone of overlap, and the latest author to analyze the problem [*94*] proposed that they be considered a single polytypic species.

Genus *Ceyx* (part, Figure 18)

The Variable Dwarf Kingfisher *(Ceyx lepidus)* is a small, insectivorous bird of forest, wooded rivers, and swift mountain streams. It also occurs in open country far from streams, even in the dry season [*5*]. Its range from the Philippines to the Solomons embraces hundreds of islands, and its numerous races vary greatly in plumage and bill color and shape. Yet they all whistle sibilantly, perch low down in the shaded interior of forest, sometimes but not



Figures 18 *(left)* and 19 *(right)*. Distribution of two species of the genus *Ceyx* (Figure 18) and three species of the genus *Corythornis* (Figure 19). Figure 18 shows **1**, *C. lepidus*, Variable Dwarf Kingfisher *(15)*; **2**, *C. argentatus*, Silvery Kingfisher *(2)*. Races of *C. lepidus* shown are *cajeli* **(1a)** and *meeki* **(1b)**. Figure 19 shows **1**, *C. leucogaster*, White-bellied Kingfisher *(3)*; **2**, *C. cristatus*, Malachite Kingfisher *(4)*; **3**, *C. vintsioides*, Madagascar Malachite Kingfisher *(monotypic)*. Species **2** and **3** constitute a superspecies.

always near small streams, and characteristically fly slowly with rapid wingbeats (J. M. Diamond, pers. commun.).

The northwestern populations of the Philippines and Moluccas look quite like the *C. lecontei* group of species. They are mainly ultramarine above and rufous below and have the rather dorsoventrally flattened vermilion bills typical of the genus and broadly associated in the family Alcedinidae with terrestrial diets. Other races have various combinations of blue or black upperparts with blue or silvery rumps and rufous, yellow, or white underparts. The New Guinea population *(C. lepidus solitarius*, Plate 2) and most of the races to the east have black bills, which in some are laterally compressed (*solitarius, nigromaxilla* of Guadalcanal) and thus closely resemble the bills of *Alcedo, Chloroceryle*, and other fishers. Do such bills in *Ceyx* also correlate with piscivory? Rand and Gilliard [*82*], while noting the similar appearance and habits of *C. lepidus solitarius* with *Alcedo* kingfishers, reported that their 19 specimens contained only land insects and spiders. J. M. Diamond (pers. commun.) found mainly insects, rarely fish, and prawns only once. In New Britain and the Solomons he recorded a diet largely of insects, with crabs in four specimens of the red-billed race *collectoris*. According to Mayr [*65*], Solomons dwarf kingfishers feed on insects, mainly aquatic ones. H. L. Bell [*5*] records dragonflies, mayflies, and midges taken by flycatching, and tadpoles. Fragmentary as the evidence is, it suggests that the form of the bill in *C. lepidus* is not adapted to any geographical variation in diet.

The Silvery Kingfisher *(C. argentatus)* of the southern Philippines is a forest-aquatic dwarf kingfisher, reportedly with much the same biology as *C. lepidus*. It is three-toed like the latter, has a fairly wide, black bill, and black upperparts, silvery rump, buffy throat, and cobalt belly. Only the last character is not present in any subspecies of *C. lepidus*, and *C. argentatus* is more closely related to it than to its other sympatric congener, *C. melanurus*.

Genus *Corythornis* (Figure 19)

In nearly all respects, these Afrotropical kingfishers are intermediate between the genera *Ceyx*, small deep-forest-dwelling "insectivores," and *Alcedo*, larger riverine piscivores. The Malachite Kingfisher *(C. cristatus)* and the Madagascar Malachite Kingfisher *(C. vintsioides)* comprise a superspecies living on lake shores, reedy streams, and swamps in savannas, and are very closely related with the White-bellied Kingfisher *(C. leucogaster)* of the forest. In brief, they resemble the African *Ceyx* species in plumage but are more aquatic in behavior and diet, and their bills are laterally compressed but red (black in *C. vintsioides*). I have discussed their biology and affinities at length in a complementary paper [*37*] to which I refer the reader for further detail.

Genus *Alcedo* (part, Figure 20)

These four may represent a branch of primitive *Alcedo* stock which gave rise to the more successful, far-flung group of seven species discussed next. They inhabit forested rivers and sluggish streams wide enough to break the forest canopy; in New Guinea the Little Kingfisher *(A. pusilla)* forages from low shrubbery over water in swamps, rivers, and lakes; but in Australia its chief habitat is mangroves. The Small Blue Kingfisher *(A. caerulescens)* also is a mangrove bird.

In keeping with their habitats, all four species have mainly aquatic diets, diving into water for insects and fish, with the larger Blue-banded Kingfisher *(A. euryzona)* also taking crustaceans and lizards [*97*]. They dig nest tunnels into sandy banks of streams or into mud between mangrove roots. The

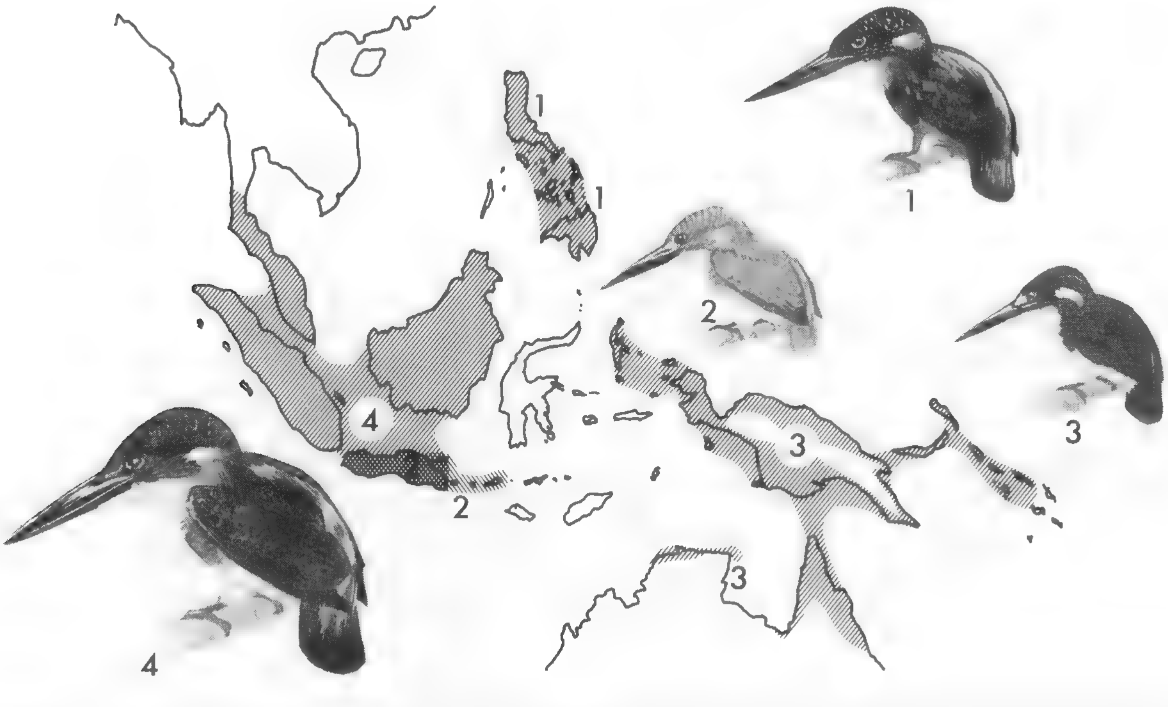


Figure 20. Distribution of four species of the genus *Alcedo*. **1**, *A. cyanopecta*, Philippine Pectoral Kingfisher *(2)*; **2**, *A. caerulescens*, Small Blue Kingfisher *(monotypic)*; **3**, *A. pusilla*, Little Kingfisher *(9)*; **4**, *A. euryzona*, Blue-banded Kingfisher *(2)*. Species **2** and **3** constitute a superspecies.

voices are thin or shrill high-pitched whistles given in flight, which is arrow-like, faster than in *Ceyx* species.

The Philippine Pectoral Kingfisher *(A. cyanopecta)* which Wolters [*109*] placed in the same subgenus as *Ceyx lepidus* and *C. argentatus*, is sexually dimorphic, the male (Figure 20) having two pectoral bands and the female one. It and *A. pusilla* are three-toed, and *A. caerulescens* and *A. euryzona* are four-toed. Toe-count is diagnostically unreliable among kingfishers [*18, 37*]; and in my view *A. pusilla* and *A. caerulescens* comprise a superspecies because of similarities in both plumage and biology. *A. euryzona* is markedly dimorphic, the male with blue-banded white underparts (Figure 20) and the female all-rufous below. Females also have more red in the bill than males; in that character, as well as in plumage, they bear a strong resemblance with the *Alcedo* species of the following group.

The genera *Ceyx* and *Alcedo* were formerly differentiated by toe-count. As presently constructed, *Alcedo* may still be separated from *Ceyx* by the possession of dusky juvenal plumages, some sexual dichromatism, and transverse bands on the crown. *Alcedo*, however, can also be characterized ecologically, for it shuns the dark interior of closed forest, living in well-illuminated, open waterside situations, and feeding from water more than from land.

Genus *Alcedo* (part, Figure 21)

The habitats of these species are much like those of the preceding *Alcedo* kingfishers: brooks in primary forest, broad rivers with dense riparian vegetation, and sometimes mangroves *(A. quadribrachys, A. meninting)*; sluggish rivers, wooded swamps, creeks and mangroves *(A. azurea, A. websteri)*; and shady streams in dense evergreen jungle *(A. hercules)*. From more open habitats than these in the tropics (in New Guinea mainly sea-shores, coral islands, and river-mouths [*5*]), the Eurasian Kingfisher *(A. atthis)* extends farther north than any other Old World kingfisher and lives in open country beside clear water of all kinds: ditches, canals, rivers, and lakes. It nests in sand or clay riverbanks with dense or sparse shrub cover, preferring slow-flowing water and avoiding roiling streams. A migrant in many northern areas of its breeding range, *A. atthis* moves in winter to temperate estuaries, salt-marshes, rocky coasts, or harbors, or to tropical ponds in open country, paddyfields, and mangroves. West European populations are more sedentary, however, and dispersal results in part from their territorial behavior [*42, 73*]. Its African allospecies the Half-collared Kingfisher *(A. semitorquata)* is less catholic, and is restricted to savanna rivers and fast-flowing streams with well-timbered banks. It is the Malachite Kingfisher *(Corythornis cristatus)* there which is the widespread inhabitant of all types of open country, and in southern Africa it migrates to the coast in winter and fishes along rocky sandstone coasts quite devoid of shrubby vegetation (E. Blake, pers. commun.).

These kingfishers prey mainly on fish but also eat other small animals taken chiefly or exclusively from water. Detailed information is available only for *Alcedo atthis*, the most widespread and probably the most abundant member of its family. Like its congeners, Eurasian kingfishers watch for animals from a suitable perch in vegetation overhanging water, make a sudden steep plunge, and capture the prey in the bill, carrying it lengthwise, head first back to the perch for beating (if the prey is large). They also dive often from hovering flight, with the body held almost vertical, and are the

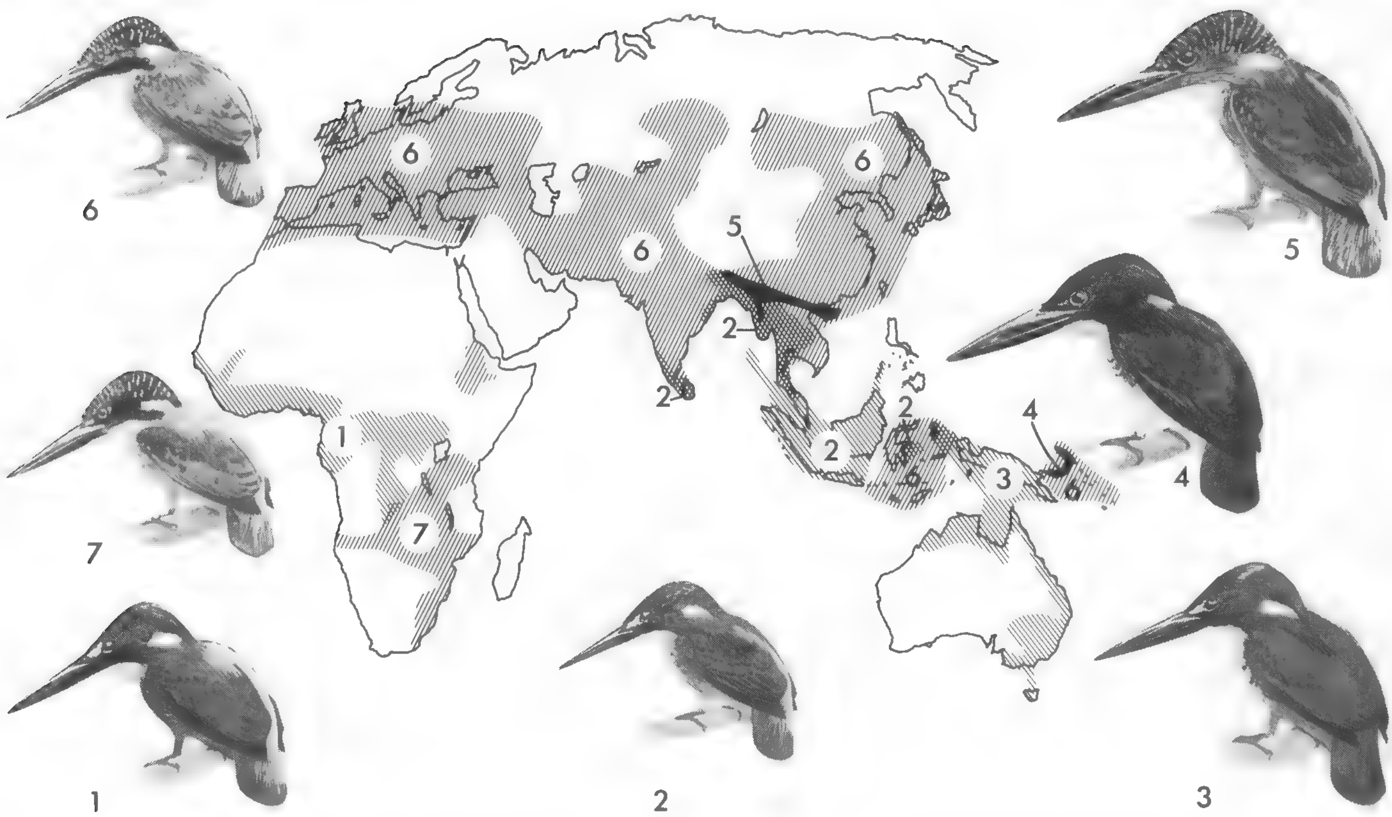


Figure 21. Distribution of seven species of the genus *Alcedo*. **1**, *A. quadribrachys*, Shining-blue Kingfisher *(2)*; **2**, *A. meninting*, Deep Blue Kingfisher *(10)*; **3**, *A. azurea*, Azure Kingfisher *(8)*; **4**, *A. websteri*, Bismarck Kingfisher *(monotypic)*; **5**, *A. hercules*, Great Blue Kingfisher *(monotypic)*; **6**, *A. atthis*, Eurasian Kingfisher *(9)*; **7**, *A. semitorquata*, Half-collared Kingfisher *(monotypic)*. Species **1** through **4** constitute a superspecies; species **6** and **7** constitute another superspecies.

only *Alcedo* species to do so. Pring-Mill [*80*] studied this species in Kashmir, and found that, while only three percent of the dives were from a hovering position, the catching success rate was 1.4 times better in hover-dives than in perch-dives.

Collinge [*16*] examined debris in 120 British nests of *A. atthis*, and contents of 80 stomachs and regurgitated pellets. By volume, fish averaged 61 percent throughout the year, the highest monthly values being 80 percent in winter (November), and the lowest 41 percent in summer (June). Insects averaged 21 percent and varied from 8 percent in winter to 27 percent in summer. Remaining annual average values were: Crustacea, 5 percent; Mollusca, 5 percent; tadpoles, 4 percent; worms and miscellaneous prey, 4 percent. Diverse fish species are eaten, easily the most abundant in Britain, being Minnows *(Phoxinus phoxinus)* and sticklebacks *(Gasterosteus aculeatus, Pungitius pungitius)*. In Kashmir the mean fish prey length was 23 mm [*80*], but a young Pike *(Esox lucius)* 125 mm long has also been recorded as prey. The insects and Crustacea referred to by Collinge were evidently all aquatic (odonate nymphs, water beetles, etc.), and the "worms" that he recorded probably belonged to one of four freshwater families and were not terrestrial earthworms. On rare occasions Eurasian kingfishers will, however, feed on dry land, and they have been recorded catching spiders, or lizards on sand-dunes [*91*], flycatching from hovering flight, and in hard winters taking garden scraps and dead fish on the ground.

Breeding biology of the other six kingfishers in this group, so far as it is known, appears to be like that of *Alcedo atthis*. The sexes of *A. atthis* are alike except that females generally have more red than males at the base of the mandible. Courtship behavior, only rarely observed and not yet adequately described, involves a wavering, butterfly-like song-flight and, when perched, mutual bowing, neck-stretching, and wing-fanning [*38, 44, 64*]. The song is a rapid series of varied warbles and high-pitched whistles, lasting for 1 to 2 seconds. Pairs are territorial. Both sexes excavate a tunnel 0.5 to 1 meter long in a vertical bank, usually by water but sometimes up to 1 km away. Rarely, they have also used tree-hollows, holes in rotten fence-posts, crevices in walls, and rabbit-burrows. Throughout Europe and Russia the usual clutch is six to seven eggs; both sexes incubate, but the male does not feed the brood [*19*]. As a rule, females lay a second clutch and both sexes begin the post-breeding molt before the second brood fledges. The incubation period is 19 to 21 days and the fledging period 22 to 26 days and abnormally as much as 37 days [*14*].

In plumage the Shining-blue *(A. quadribrachys)*, Deep Blue *(A. meninting)*, and Azure *(A. azurea)* Kingfishers are much alike, deep blue above and cinnamon below. The first two are three-toed and azure-backed, appear to have identical diets and habitats, and comprise a superspecies, the African *A. quadribrachys* being about twice the weight of the Oriental *A. meninting*. *A. azurea* of New Guinea and Australia is the same size as *A. quadribrachys*, and so similar to it that skins can be safely distinguished by only two features: *A. azurea* is ultramarine-, not azure-backed, and has four toes. The cream and dark blue Bismarck Kingfisher *(A. websteri)* of the Bismarck Archipelago is a parapatric allospecies of *A. azurea* [*89*]. In turn *A. azurea* is parapatric with *A. meninting*, and despite their toe-count difference, should be regarded as belonging to the same superspecies [*37*]. Another character common to the four allospecies is their dark juvenal plumages, described by Schodde and Mason [*89*] for *A. azurea*.

Alcedo atthis is markedly disjunct in the Malesian part of its great range (Figure 21). For the most part it is parapatric with the *A. meninting* superspecies there, the largest region of sympatry being on mainland Asia. *A. atthis* probably is excluded from New Guinea by competition with *A. azurea*, and from the Bornean region by competition with *A. meninting* and with *A. euryzona*. In Africa *A. semitorquata* forms a superspecies with *A. atthis* (some authors have regarded them as conspecific) and, significantly, it is parapatric with the African representative of the *A. meninting* superspecies [*36*].

The Great Blue Kingfisher *(Alcedo hercules)* is a large version of *A. atthis* and is sympatric with it.

In summary, the seven species in this group comprise two essentially parapatric superspecies *(A. meninting* supersp., *A. atthis* supersp.) and one monotypic species *(A. hercules)*, which is an ally of *A. euryzona*. In the few areas where any two of these species occur together (cross-hatched in Figure 21), the larger one weighs at least 1.5 times the smaller (Figure 6), suggesting that a suitable size difference has to be evolved before the species can invade each others' ranges, or that size differences become greater when two species are confronted with competitive interactions for the same kind of food.

Subfamily Cerylinae

Genus *Chloroceryle* (Figure 22)

A better example of the tendency for congeneric kingfishers to differ substantially in size where their ranges overlap is provided by the green kingfishers *Chloroceryle* of the Neotropics. Each species is sexually dimor-

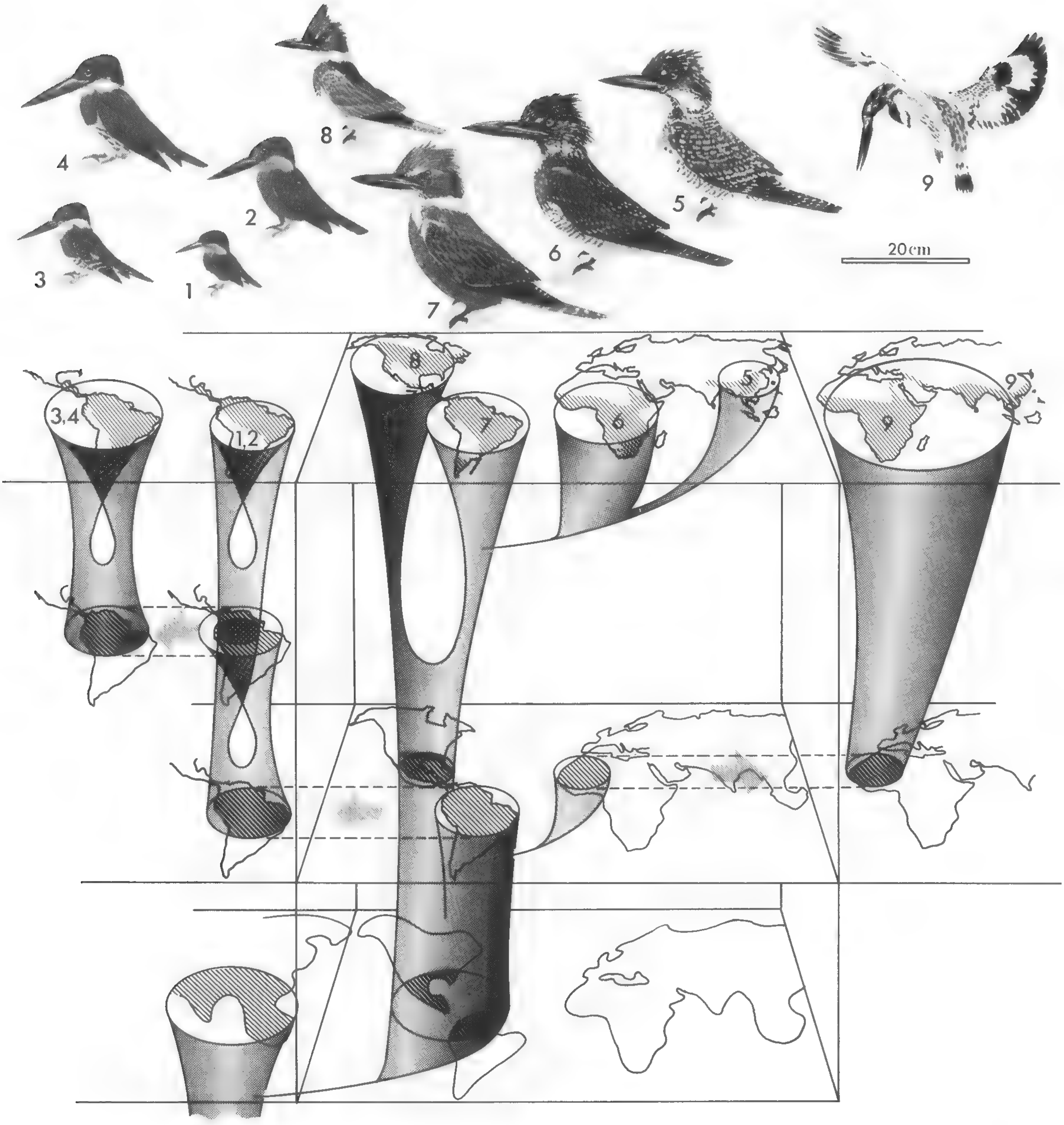


Figure 22. A putative phylogeny of ceryline kingfishers. The box is a transparent house in which the floors are latitude and longitude and height is time. The roof shows the modern world with the distribution of each species indicated roughly as a circle (ellipse in the perspective), and the actual ranges detailed by hatching. For clarity, *Chloroceryle* and *Ceryle* are displaced to the left and right, respectively, of the house and mapped on extensions of the first floor and roof. The ground floor represents the Pliocene, the first floor the early Pleistocene, and the roof the present. The model implies a pre- or early-Pliocene invasion of the New World from the Oriental Region (ground floor at left) via Beringia, and separate Pliocene and Pleistocene trans-Atlantic invasions of the Paleotropics. Species are the following: **1**, *Chloroceryle aenea*, American Pygmy Kingfisher, ♂ *(2)*; **2**, *C. inda*, Green-and-rufous Kingfisher, ♂ *(2)*; **3**, *C. americana*, Green Kingfisher, ♂ *(8)*; **4**, *C. amazona*, Amazon Kingfisher, ♂ *(2)*; **5**, *Megaceryle lugubris*, Crested Kingfisher, ♂ *(3)*; **6**, *M. maxima*, Giant Kingfisher, ♂ *(2)*; **7**, *M. torquata*, Ringed Kingfisher, ♂ *(3)*; **8**, *M. alcyon*, Belted Kingfisher, ♂ *(2)*; **9**, *Ceryle rudis*, Pied Kingfisher, ♂ *(4)*. Species **5** through **8** constitute a superspecies.

Figure 23. Tropical riverine forest habitat of the Green Kingfisher *(Chloroceryle americana)*, Amazon Kingfisher *(C. amazona)*, and Ringed Kingfisher *(Megaceryle torquata)*, Rio Suia Missu, Mato Grosso, Brazil.

phic, and in plumage they fall clearly into two groups, suggesting dichotomous evolution from a single ancestor (Figure 22). In the smallest *(C. aenea)* and the second largest *(C. inda)* both males and females are very similar; and the same applies to the second smallest *(C. americana)* and the largest species *(C. amazona)*. All four inhabit forest streams (Figure 23) and are exclusively fish-eaters, so they probably would compete very strongly with each other were it not for their different sizes.

I captured a small sample of all four species at a locality in Mato Grosso State, Brazil, and their average bill lengths were in the ratio 1 to 1.5 to 1.9 to 2.5 (samples of 9, 4, 4, and 1 respectively). Specific wing-lengths were in much the same ratio, 1 to 1.4 to 1.8 to 2.3. Congeneric animals which are sympatric tend to differ in linear measurements—particularly those of their feeding structures—by a factor (Hutchinson's Constant) of 1.28 [*63*], and that value is approached closely by the green kingfishers. *C. americana* exceeds *C. aenea* by a factor of 1.50 (bill) and 1.40 (wing); *C. inda* exceeds *C. americana* by 1.27 and 1.29; and *C. amazona* exceeds *C. inda* by 1.32 and 1.27. In general, weight is a better measure of size differences between species than linear measurement. Mean weights of the Mato Grosso sample were in the proportions 1 to 2 to 4.5 to 8 (*C. aenea* 12.7 g, *C. americana* 27.2 g, *C. inda* 59.1 g, *C. amazona* 98.0 g); and at a Bolivian locality, J. V. Remsen (pers. commun.) obtained the proportions 1 to 3 to 4 to 10 from a sample the same size as mine. Pooling 60 *Chloroceryle* weights from various places gives an overall ratio of 1 to 2.6 to 4.1 to 9.2, but it should be noted in Figure 6 that the highly polytypic *C. americana* varies far more (the heaviest being 2.3 times the lightest) than any of the other three species, in which the heaviest individuals are respectively 1.4, 1.4, and 1.5 times the lightest ones. From smaller to larger, the species differ in weight by factors of 2.64, 1.56, and

Figure 24. Habitat of the Belted Kingfisher *(Megaceryle alcyon)*, Banff National Park, Alberta, Canada.

2.21, with an average of 2.14 approximating the cube of Hutchinson's Constant which is 2.10.

The green kingfishers are entirely aquatic by habitat and diet and there is only one authenticated case of insectivory (terrestrial), in *C. aenea*. They feed by diving from perches, but the two larger species also dive from hovering flight, commonly in *C. amazona*, less so in *C. americana*. The larger the kingfisher, the higher its mean perch height above the water, and the greater its mean prey size (J. V. Remsen, pers. commun.). *C. aenea* and *C. inda*, the smaller species-pair, prefer deeply shaded waterways and inhabit mangroves, swampy forest, wooded small ponds, and forest streams, and I have netted each of them over such tiny streams in dense gallery forest that I doubted whether at least the large *C. inda* could have found much of its food there. Their habitat requirements restrict both species to the tropics. The larger species-pair inhabits more open waters in the forested lowlands, lakes and marshes in the savannas, and even mountain torrents at 2,500 meters. Their ranges extend far south and north *(C. americana* only) of the tropics. J. V. Remson (in prep.) has recently completed a study of the zoogeography and community ecology of the genus.

Skutch's [*95*] detailed account of the Amazon Kingfisher and his observations on the Green Kingfisher (*in* Bent [7]) indicate that the biology of *Chloroceryle* does not differ importantly from that of other bank-nesting kingfishers. He described a greeting ceremony by the male, perching by his mate and raising his wings above his back for a few seconds, like that described for *Alcedo atthis*; moreover, like that Old World fisher, the green kingfishers have a song. It is alike in all four species (J. V. Remsen, pers. commun.) and consists of a rapid series of sharp notes, ascending in pitch and increasing in tempo, then falling in both pitch and tempo.

Genus *Megaceryle*

These are shaggily crested fishers with marked sexual dimorphism; the New World species are blue-gray dorsally and the Old World blackish. Figure 22 illustrates males. The female Belted Kingfisher *(M. alcyon)* has a gray breast band like the male and also a second, rufous band. The Ringed Kingfisher *(M. torquata)* is rufous below, with a rufous breast in the male and gray in the female. In the Giant Kingfisher *(M. maxima)* the male has a rufous breast and whitish belly, the pattern being reversed in the female; and in the Crested Kingfisher *(M. lugubris)* the male's vestigial rufous breast band is the only pattern of color on the whitish underparts.

At 300 to 400 grams, the Neotropical and the African species are quite the largest fishers. They are found throughout the lowland savannas and within the rainforest, where they inhabit timbered streams and lakeshores, and broad rivers with reaches of exposed sand. The banks in which they nest are densely shaded by overhanging trees. They are found also in mangrove lagoons and sometimes on the coast, but never far from shady trees. The Crested Kingfisher *(M. lugubris)* is rather smaller and occurs in winter on large lowland streams and in summer up to 2,100 meters on mountain torrents and rocky streams with overgrown, timbered banks. None of these three is known to hover when fishing, and all are rather shy and secretive birds. Still smaller is the familiar North American Belted Kingfisher *(M. alcyon)*, a less wary bird of open waters, common and much better known than its tropical and sub-tropical congeners. It occupies all types of waters from estuaries and bays to lakes (Figure 24) and rocky, swift mountain streams, and it needs shady vegetation less than the other species do. As with the same-sized *Chloroceryle amazona*, Belted Kingfishers often hover when fishing, scanning clear water from as great a height as 10 to 12 meters and making a straight or spiral dive directly downward [7]. Fish predominate in the diets of all species except *M. maxima*, which evidently feeds largely on river crabs [2]. They also take frogs *(M. maxima, M. torquata)*, and small aquatic reptiles *(M. torquata)*, while for *M. alcyon* Bent listed in addition mussels, clams and oysters, salamanders, young land birds, mice, a variety of terrestrial insects, including moths and butterflies taken on the wing, and even, in hard weather, fruits of such trees as Tupelo, *Nyssa aquatica*.

Megaceryle kingfishers generally live solitarily or in pairs, but they nest semi-colonially when concentrated by a paucity of suitable banks and cliffs. All species have a loud, rattling call of *kek* notes. All that has been described by way of courtship is a pair or small group "tumbling and wheeling" in the air, "gyrating above the water" [7] while calling loudly. Pairs dig nest holes 1 to 2.5 meters long, usually in a cliff near water, but sometimes in distant gullies, sand-pits, or road-cuttings. Exceptionally, *M. alcyon* nests in tree cavities and decaying *Nyssa* stumps [7]. Species in this genus are monogamous; they raise only one brood a year, but may lay repeat clutches [*19*]. Incubation regimes were detailed by Skutch [*96*] for *M. torquata*, and the growth of nestlings by Dowsett [*31*] for *M. maxima*.

In a morphological analysis of cerylines Miller [*69*] concluded that within the genus *Megaceryle, M. alcyon* is most nearly allied to *M. torquata; M. torquata* is intermediate between *M. alcyon* and the Old World species; the African *M. maxima* is intermediate between the two New World species and *M. lugubris*; and the nearest ally of *M. lugubris* is unquestionably *M. maxima*. I have been able to study all four species in the field and arrived at the same conclusion independently; they are sufficiently closely related to constitute allospecies of a single superspecies. Figure 22 shows the evolutionary interpretation that seems to account most satisfactorily for the present-day ranges and evident affinities of the *Megaceryle* species.

Pied Kingfisher (Figures 22 and 25)

Fishing from a hovering flight has been developed by the Pied Kingfisher *(Ceryle rudis)* to the extent that under some weather conditions it is the principal method of hunting. This distinctive and sexually dimorphic species (Figure 25) is common on open and slow-moving waters in Africa

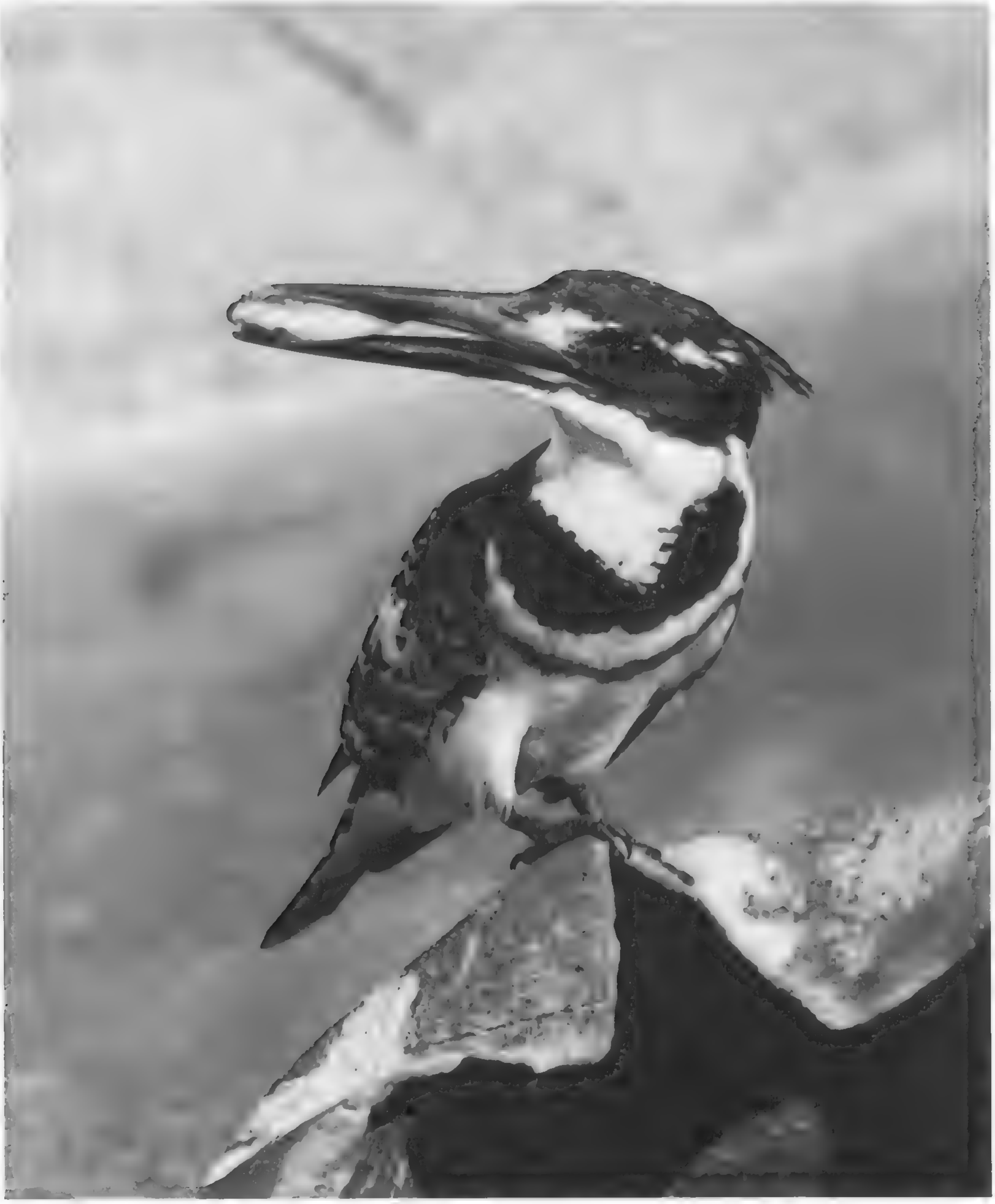


Figure 25. Male Pied Kingfisher *(Ceryle rudis)*, Rhodesia. Photograph by Peter Steyn.

and southern Asia, mainly frequenting freshwater below 500 meters in altitude and, in Asia, also estuaries and other brackish waters. It is highly conspicuous and vociferous and its fishing is spectacular. It shuns shade and fishes the open water, usually along lakeshores and rivers, up to 3 km offshore in Lake Kariba [*53*]. In calm weather 80 percent of its dives are made from perches and 20 percent from hovering flight, which is commonly as high as 10 meters; but when it is windy—the usual condition on the great lakes of Africa—the proportions are reversed [*29*]. About half of all dives are successful. In Kashmir Pring-Mill [*80*] found hovering rather more successful than perching and in Uganda Douthwaite [*29*] found the converse. The last author showed that termites, caught on the wing, are regularly preyed upon, and he also found a few grasshoppers in regurgitated pellets. Apart from these exceptions, Pied Kingfishers hunt entirely in water. Mukherjee [*74*] shot 300 adults in the brackish Sundarban in West Bengal and found that 57 percent of the diet by weight were fish, of which three-quarters numerically were *Puntius* sp., *Mystus* sp., *Mugil parsia*, and *Ambassis* sp.; 17 percent were decapod crustaceans; and 26 percent large aquatic insects. Evidently all the arthropods were taken from water, including the surface in the case of water-boatmen Gyrinidae, not from land or the air. Since kingfishers, or at least *Megaceryle alcyon*, can partly digest bone [*88*] but not arthropod chitin, Mukherjee's values probably exaggerate the weight of decapods and insects eaten by Pied Kingfishers. In Africa the bird is almost exclusively a fish-eater. On Lake St. Lucia, Natal, 80 percent of the fish diet was *Sarotherodon mossambicus*, fishes in the 1 to 2 gram weight-class being captured most often [*107*]. On Lake Victoria 70 to 80 percent of its diet was the commercial *Haplochromis* (median length of 80 mm) and 20 to 30 percent was *Engraulicypris argenteus* [*29*]. The Pied Kingfisher consumes about 44 grams, or half its weight, each day and may capture individual fish weighing up to 15 grams. Diet is related to the vertical and horizontal distribution of prey fish [*107*]. In Lake Kariba the birds hunt far offshore at dawn and dusk for the introduced sardine *Limnothrissa miodon*, a pelagic fish which rises to the surface only at those times [*53*].

Pied Kingfishers are the only "pelagic" fishers. They hover to a much greater extent than any other species. Uniquely, they can swallow fish less than 20 mm long on the wing, without having to return to a firm perch for beating, as they do with larger prey. They have even been known to catch two fish in one dive [*106*]. Clearly, this is the most specialized fisher of its family.

Population density in the Pied Kingfisher varies from a norm of about two up to sixteen birds per km of shoreline or river [*28*]. Where it is high, breeding may be semi-colonial. Nest tunnels are generally excavated in sand- and mud-cliffs, in the absence of which they may be dug in man-made banks up to 3 km from water [*30, 100*]. Nesting is preceded by noisy aerial chases involving two to eight birds, and by group displays on bare ground by both sexes [*30*]. Ten calls having as many distinct functions have been described. Many nests have one to five helpers, always male [*30*], and Reyer [*84*] distinguishes primary helpers which feed their own siblings of later broods, and secondary helpers which feed unrelated young. By radio-tracking pairs and helpers, he has been able to calculate their time and energy budgets and to predict the breeding success of pairs with varying numbers of helpers. His observations of breeding success conform with the prediction, suggesting that cooperative breeding in Pied Kingfishers is a flexible means of adapting to immediate ecological conditions.

Geographical Origin and Radiation

By far the greatest density of kingfisher species occurs in Malesia (Figure 1). The region includes Sumatra, Java, Borneo, and adjacent continental Asia south of the Tropic of Cancer, the Philippines, Sulawesi, the Moluccas, the Lesser Sundas and other islands around the Banda Sea, and the Papuan subregion of New Guinea and its offshore islands together with the Bismarcks. Forty-nine species, or 57 percent, of the world's kingfishers are resident here. Moreover, many of these Malesian kingfishers are relatively primitive, considering their generalized diet and unspecialized mode of foraging, their ancient, stable habitat of equatorial rainforest, and their being oligotypic (i.e., of a genus having a few species; or of a species having few subspecies) and systematically isolated [*37*]. Hardly any similarly primitive forms occur elsewhere, leaving the Malesian region as the likely center of origin of the family, although such a conclusion made in the absence of confirmatory fossil evidence may prove erroneous. For example, Chapman [*11*], in a zoogeographical analysis which is a classic of its kind, concluded that the Neotropical family of motmots originated in Oligocene Central America from where they invaded South America at least three times. He also inferred that the todies, peculiar to the Caribbean, arose from motmots in Central America. Palaeontological evidence now shows that the present distribution of both families are relict. *Protornis glaronensis* from the lower Oligocene of Switzerland, placed by Peyer [*79*] in the Alcedinidae near to the genus *Dacelo*, has been re-examined by Olson [*75*], who concluded that it is a genus of motmots. Thus the Momotidae arose not in the New World at all, but in the Old. Olson also showed that *Palaeotodus* of the middle Oligocene of Wyoming is a tody, so that the family Todidae may have arisen 20 to 25 degrees farther north than Chapman thought. This analysis emphasizes the need for caution in locating the origin of kingfishers, particularly since, with the removal of *Protornis* from the Alcedinidae, we are left with no ancient fossils which would indicate the provenance of the family indisputably. The remaining fossil kingfishers are neospecies, and only one, a specimen of *Megaceryle maxima* from the Pleistocene of Israel, occurred outside its present range [*8*].

Outside Malesia the only regions with notable numbers of kingfisher species are the Pacific with 11 to 14 residents of which 7 are endemics, and Africa with 16 residents of which 14 are endemics. The African species and the two from Madagascar appear to be relative newcomers to the Afrotropical Region, probably in the Pliocene and Pleistocene. They are the product of no fewer than 9 or even 12 separate invasions, mostly from Asia, and have undergone only modest subsequent speciation within the Region [*37*].

Some evidence has been given above that Pacific, Australian, and Palaearctic kingfishers likewise are all the products of centrifugal differentiation of Malesian stock; but that does not mean that the family necessarily originated in that part of the world alone. The coraciiform families clearly have an ancient history in the Palaeotropics [*35*] and the Alcedinidae might have arisen broadly throughout the ancient Paleotropics rather than just in the region where Australia was converging with southeast Asia. There is some evidence for the wholesale annihilation of rainforest in Pleistocene Africa [*43*]. It is difficult, otherwise, to account for the fact that Africa has an avifauna two-thirds, and a flora only two-fifths, the size of those of South America [*86*]. Such elimination of rainforest would have extinguished any surviving primitive forest-dwelling kingfishers, making it impossible to assert that the Afrotropics were not anciently inhabited by alcedinids.

However, there remains one further fact which strongly suggests that kingfishers originated in Malesia alone, and not broadly throughout the Paleotropics. It is the absence in Africa of nonforest kingfishers which are systematically isolated. Were African savanna species difficult to relate with Malesian alcedinids or their Asiatic derivatives, one might reasonably infer that they arose from primitive African rainforest stock (subsequently extinguished). Since, in fact, African nonforest kingfishers all appear to be related to Oriental forms that themselves appear to have originated in Malesia, I conclude that the Afrotropics were not a primary landscape in the early evolution of the family and that kingfishers arose solely in Malesia.

From primitive stock in Malesia, the subfamilies Daceloninae and Alcedininae differentiated and each radiated in all directions, except that only dacelonines penetrated Micronesia and Polynesia, where they have speciated quite recently and plentifully. Dacelonines are much more numerous and diverse than alcedinines in New Guinea, and there is some substance to the view that originally the dacelonines belonged to the tropics of the ancient continent of Sahul and the alcedinines to Sunda, respectively—the southeast and the northwest extremities of the region which became Malesia [*1*]. Dacelonines have done much better than alcedinines in Australia, producing an endemic halcyon there and a kookaburra, the latter being a good example of centrifugal derivation from Malesian rainforest congeners [*85*]. To the northwest, invasion of Asia and thence Africa by dacelonines has been limited. Apart from the Malesian *Halcyon coromanda* and *H. capensis* which range widely into India, and from the littoral *H. chloris* which is clearly a very recent arrival as far west as Africa, the Asiatic and African tree-kingfishers comprise ten closely allied woodland species which probably represent a single primordial incursion into Asia. The dacelonines have barely entered the Palearctic; four species are represented there peripherally. Alcedinines, and the Cerylinae to which they probably gave rise, have fared conspicuously better in Asia, Africa, and of course America, and are considerably more diversified ecologically there (particularly in Africa, with its dry-land species of *Ceyx* and *Corythornis* and its cerylines) than they are in Malesia. With *Alcedo atthis, Megaceryle alcyon*, and *M. lugubris* in the Holarctic, the alcedinines and cerylines have proved more successful colonists of postglacial habitats than have the dacelonines. Conceivably, it was such a cold-climate fisher in northwest Asia which crossed the Bering Straits to penetrate the Americas, giving rise to *Chloroceryle* and *Megaceryle* (Figure 22).

Evolution of Habitat, Foraging, and Diet

A common method of foraging in kingfishers involves the quiet surveillance of their surroundings from a branch, then a swoop or dive onto their intended prey. While not very versatile, this method enables most species to catch a considerable variety of animals. Typically, and perhaps primitively, kingfishers take prey from the ground and near the surface of shaded water. The prey consists of invertebrates and small vertebrates which are still or slow-moving; kingfishers do not give chase. Various derivative lineages of kingfishers have emphasized one or another component in this generalized diet and in doing so have evolved marked specializations. I wish to draw a primary distinction between dry-land and aquatic foraging.

Exclusively dry-land predators are the genera *Cittura, Tanysiptera, Melidora, Clytoceyx, Dacelo* and *Lacedo*, and some species of *Halcyon* (southeastern members of the *H. macleayii* superspecies, the yellow-billed kingfishers and *H. pyrrhopygia*). At the other extreme, *Alcedo* and the Cerylinae feed almost exclusively from water. Intermediate conditions are found in the genera *Actenoides, Ceyx*, and *Corythornis* and in some 27 halcyons; each species is both a land and water feeder, but only a few may take as much as half of their diet from water (the storkbills, *H. smyrnensis, H. pileata, H. senegaloides, H. saurophaga*). Throughout the family there is some correlation between specific diets, foraging behavior, and habitat.

Land and Intermediate Foragers

This group embraces all of the tree-kingfishers (Daceloninae) and the alcedinine genera *Ceyx* and *Corythornis*, some 66 species in all. Most are birds of the interior of tropical rainforest or other biomes with dense, woody vegetation: mangroves, montane forest, and lowland savanna woods. In a specialized mode of foraging, some rainforest species shovel into ground-litter and moist, loose soil to expose invertebrates *(Halcyon farquheri, H. smyrnensis*; the nocturnal *Melidora macrorhina*; and the extraordinary *Clytoceyx rex)*.

A minority of these 66 species inhabit open country, and evidently they have evolved into it from ancestral populations in rainforest. Kookaburras provide the best evidence for the progression, from New Guinea rainforest through woodlands to open savannas in Australia, and in the process they have become large and powerful predators of terrestrial vertebrates. In Africa the halcyons mostly inhabit open savanna woodlands, and although some are quite large they have not evolved as predators to the same extent as have the savanna kookaburras. The small *H. chelicuti* has the most open, even arid habitat of any African kingfisher. It and the kookaburra *Dacelo gigas* have cooperative social organizations, probably a correlate of their very open habitats. Also in the Afrotropics is a savanna species of *Ceyx* which almost certainly arose from rainforest ancestors, and two species of *Corythornis*, found at watery places in savannas, which probably did likewise [*37*].

Particularly instructive with regard to habitat evolution is the subgenus *Todiramphus* of *Halcyon* kingfishers. Clearly its center of origin is New Guinea, where the dominant biome is, and always has been, rainforest; at least half of its 20 species inhabit rainforest there. Others occupy more open habitats, in extreme cases beaches *(H. chloris, H. saurophaga)* and arid savannas *(H. pyrrhopygia)*, and have presumably evolved into such habitats from rainforest. That the evolutionary progression can also proceed in the opposite direction, from open to closed habitats, is evidenced by the three species endemic to distant volcanic islands in the Pacific and by *H. farquheri* of the New Hebrides. All inhabit primary forest; but New Guinea rainforest kingfishers seem far less likely than seashore ones to colonize distant islands. The four Pacific endemics have probably shifted to their forest habitat from seashore or open-habitat colonists, evolving as flat-billed, sallying flycatchers in the process. Evidently ancestral *H. sancta* was the colonist concerned, and it probably adapted to open habitats while undergoing speciation in Australasia.

Perhaps it was the same ancestral population which gave rise to *H. chloris*, a highly successful long-distance colonist and one of the "great speciators" [*24*]. *H. chloris* generally frequents open coastal vegetation, but in the absence of forest-dwelling congeners it will invade closed forest, as on those New Hebridean islands not inhabited by *H. farquheri* [*25*]. Presumably a second colonization of an island by coastal *H. chloris* can occur only when competition is minimized by the original colonist having adapted to forest habitat, as on Palau Island and the Lesser Sundas.

As already argued, *H. farquheri*, too, is probably secondarily a forest bird. Halcyons of this subgenus inhabiting more open habitats obtain a greater porportion of their food from water than do the others. I anticipate that that will prove to be the case in particular with the Beach Kingfisher *(H. saurophaga)*, which is evidently as aquatic as the water-foraging alcedinines and cerylines. Significantly, this bird adumbrates the important grade of organization innovated by those subfamilies by being the only one that hovers of the 66 land and intermediate feeders.

Water Foragers

There are 20 fishers proper, all 11 species of *Alcedo* and the 9 cerylines; and although some of them are known to take prey from dry land and from the air, such food provides only a tiny proportion of diets which are otherwise entirely aquatic. All *Alcedo* species but two inhabit tropical forested waterways and are not known to fish by diving from hovering flight. The two exceptions are the temperate zone *A. atthis* and its African allospecies *A. semitorquata*, which inhabit all manner of open waters and by no means restrict their fishing to shady situations. Dietary components of *Alcedo* species have not been quantified except for *A. atthis*, whose diet contains about 60 percent fish, twice the amount taken by one of the most piscivorous of the intermediate-category kingfishers, *Halcyon smyrnensis*. Moreover, to a small but significant extent, *Alcedo atthis* hovers.

For the most part the Cerylinae appear to be almost entirely piscivorous, although at one locality about 40 percent of the diet of *Ceryle rudis* were arthropods [*74*]. Hovering has not been reported in the smaller *Chloroceryle* species-pair, which inhabit deep-forest streams, nor in the three tropical and subtropical species of *Megaceryle*, which fish mainly at the shaded edges of rivers. But the remaining four species, living on open and unshaded waters, all hover, and *Ceryle rudis*, the only "pelagic" fisher, catches at least half of its fish by hovering.

There is clearly an evolutonary relationship among kingfishers between the three characteristics of hovering, exploitation of broad expanses of unshaded water, and a high dietary proportion of fish. The smaller *Chloroceryle* species-pair is of interest in being the only forest-zone kingfishers which are exclusively piscivorous. They do not fish open waters nor do they hover. It suggests that either, unlike other kingfishers, they have evolved as exclusive piscivores while remaining in their original tropical forest habitat; or, more likely in my view, their ancestors fished open waters, not necessarily tropical. In the latter event they will be the more derived *Chloroceryle* species, and their larger congeners the more primitive.

Summary

I have reviewed current knowledge of the kingfishers, group by group, with the emphasis on habitat, diet, and foraging behavior. Past systematic arrangements have necessarily been based mainly on morphology, and biological criteria now prompt some re-arrangement. I recognize 86 species (about 40 being allocated to 14 superspecies) in 14 genera and three subfamilies.

The Daceloninae (55 tree-kingfishers) are centered in southeast Malesia. They have strident voices and nest in tree-holes and termitaria. *Halcyon* is reconstituted by excluding six primitive species *(Actenoides)* and including the storkbills, formerly *Pelargopsis*. Most dacelonines retain the putatively primitive condition of generalized predation on animals of the rainforest-floor; but some have specialized as snail-breakers, soil-sifters, and earthworm-eaters; and others have evolved into open, dry woodland as hook-billed predators, onto tropical seashores as part-fishers, and back into forest again as flycatchers.

The 22 Alcedininae are centered in northwest Malesia. In both *Ceyx* and *Alcedo* there are three-toed and four-toed species in the same superspecies. These genera can be diagnosed, not by toe-count, but biologically: *Ceyx* feeds from the ground in unbroken rainforest and *Alcedo* feeds entirely from waterways that break the forest canopy. *Corythornis* (Afrotropics) is intermediate. All three genera are earth-bank nesters with weak voices, and each has an open country representative in tropical savannas or the temperate zone.

The nine Cerylinae are barely distinguishable biologically from the Alcedininae; they are almost entirely aquatic and several are wholly piscivorous. Their hypothetical phylogeny, with one Beringian and two trans-Atlantic invasions, is shown in Figure 22.

Originating probably in Malesian rainforest, the family has evolved into open, nonforest habitats 8 to 10 times and has invaded the Afrotropics 9 to 12 times. The most effective fishers are those of open waters that plunge-dive from hovering flight, a characteristic which has evolved in all three subfamilies.

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THE CONTRIBUTION OF THE AMATEUR TO NORTH AMERICAN ORNITHOLOGY: A HISTORICAL PERSPECTIVE

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"Since the early days of the Royal Society of London, when even chemistry and physics were represented by amateurs, one science after another has inevitably become fully professionalized, and now ornithology stands out with astronomy and very few others as a science in which the amateur tradition is still of first rate importance" [*24*]. While most other scientific disciplines have become fully professionalized, ornithology continues to attract many capable, enthusiastic non-professionals, and there is a definite movement at present to ensure their future collaboration in the activities of the science.

In the history and sociology of science, the professionalization of a discipline was considered a measure of the maturity of the field and thus a desirable process. The progressive phasing out of amateurs was a collateral development until their contributions to a particular, recently professionalized discipline became negligible and finally non-existent. Before examining the case of American ornithology, which seems to be different from the model of the professionalizing of scientific disciplines, one should consider the definitions of professional and amateur.

The term professional has been used in different ways at different times. The traditionally learned professions are those of divinity, medicine, and law, which were developed in Europe. In America, however, the term carries a broader significance. Conventionally, professions are considered as occupations requiring special training in a particular body of knowledge or a particular technique or technology. The formation of professional associations ensures high standards and encourages the advancement of knowledge [*26*]. Professionals also receive payment for services rendered. In the United States, the growth of professionalism was greatly enhanced by the development of the graduate school and the subsequent organization of university research programs between 1860 and World War One [*3*]. The professionalizing of most scientific fields in the United States was accomplished by the first half of the present century. Professional scientists working in their specialized fields can now obtain Ph.D.'s, find established positions, join scientific associations, and publish in the appropriate journals. They are members of the larger scientific community and, if fortunate, participate in the networks of "invisible colleges" [*8*]. In contrast, amateurs are regarded as dilettantes, who merely play at being scientists but generally do not contribute significantly to science.

A number of studies by historians and sociologists of science have examined how professional scientists function, noting their interactions with their peers and with scientists in other fields [*8, 16*]. Most of these studies, however, have been conducted on the completely professionalized physical sciences. Because of this orientation, it is not generally recognized that amateurs still constitute the underlying foundation of several scientific fields.

From the viewpoint of the professional-amateur relationship, ornithology is a field in which amateurs have not only maintained their influence, but still outnumber their professional counterparts and contribute considerably to the science. Not only do the non-professionals provide data and assistance to the professionals in a variety of ways, but independent amateur research projects still constitute about 12 percent of the published articles in the major American ornithological journals ([*21*]; see also Table 2). In order to understand the processes that led American ornithology to deviate from the standard view of professionalization, a brief review of the history of North American ornithology is necessary.

The Origins of a "Deviant" Science in the New World

Although the first mention of American birds is found in Columbus's journals, the first real naturalist of the New World was Gonzalo Fernandéz de Oviedo y Valdéz, whose book "Historia Natural y General de las Indias," appeared in 1535. From the 16th through the late 18th century, an increasing number of European naturalists published works based on observations and collections made in America. Society in North America at this time was still at its prescientific stage. European scientists observed a multitude of novel natural history objects, which they described, collected, and sent back to Europe for more detailed study. The observers, at least, were a product of a scientific culture that valued the systematic exploration of nature [*2*].

By the beginning of the 18th century, natural history became an important pastime for some educated, wealthy Americans, many of whom received their medical training in Europe. There, they were introduced to the most recent ideas in natural history, which was taught as an integral part of the medical curriculum in Holland and Scotland. Upon their return to North America, the newly trained physicians continued corresponding with their European colleagues and friends and spent considerable time in the field, trying to satisfy the collecting mania of European naturalists for American curiosities. They helped provide these absentee landlords of science [*12*] with valuable information which the European scientists tried to fit into the existing theoretical framework of European science. Centers of scientific inquiry in natural history arose in colonial Boston, Charleston, New York, and Philadelphia. Natural history societies in these towns became important forums for the exchange of ideas and the acquisition of scientific information.

North America was still on the periphery of scientific activity, but important advances were made toward developing an American scientific community. Although in the late 18th century many serious American naturalists still sent their contributions to the Royal Society of London, where much of their research was published, scientific journals started to appear in the New World. The first exclusively scientific periodical of the United States was Dr. Samuel Latham Mitchill's *The Medical Respository*, founded in 1797, which contained many contributions on natural history. A number of other journals were founded before the middle of the 19th century, offering alternative publication outlets for American scientists.

Well into the 19th century, ornithology was the domain of the gentleman-naturalist. Since their knowledge of birds had to be acquired by patient observation in the field, and by the study of specimens they and others collected, private ornithological collections were important in the training of the early naturalist-ornithologists. Philadelphia became the most important center of study. Philadelphian Charles Willson Peale, a painter, started a collection (or "museum" as he was fond of calling it) in 1784. By 1805 it contained 760 species of birds. The Academy of Natural Sciences of Philadelphia was founded in 1812, and by the middle of the 19th century it housed the largest ornithological collection in the world [*29*]. As ornithological education in the modern sense was non-existent, even the famous ornithologists of the early 19th century, such as Alexander Wilson and John James Audubon, had few qualifications acceptable by modern standards for being considered professional. A love of nature and a special interest in birds were the prerequisites for becoming an ornithologist. The same criteria persisted well into the second half of the century. Robert Ridgway and Frank M. Chapman, for instance, had no university training in biology but learned their "trade" as apprentices [*22*]. Positions for naturalist-ornithologists were so scarce in the early 1840's, that Spencer Fullerton Baird, who later became Assistant Secretary of the Smithsonian Institution, was warned by his elder brother (himself an enthusiastic ornithologist) not to get involved in bird study as a career, because "no means of livelihood . . . is to be obtained in America from ornithology" [*10*]. During the second half of the 19th century, more positions became available for those with a scientific interest in bird study. In fact, Baird personally was responsible for many of the part-time ornithological opportunities that were created in the early 1850's.

Ornithology as a Part-time Profession

To explore the West, the government of the United States sponsored and conducted numerous expeditions, beginning with the journeys of Lewis and Clark in 1804, during which the two leaders performed the duties of naturalists. Subsequent expeditions resulted from the surveying of the Canadian and Mexican boundaries, and surveys for various railroads. On all of these expeditions a naturalist invariably was sent along, whose tasks included the observation, description, collection, and preparation of specimens of birds from the new territories. The largest number of part-time "professional" ornithologists came from the ranks of the United States Army Medical Corps. More than three dozen surgeon-naturalists were stationed in the West and Southwest during the wars with hostile Indian tribes and with Mexico. They belong to two distinct periods. The "first generation" of surgeon-naturalists were active before the Civil War; the "second generation" of part-time professionals were active after the Civil War.

The surgeon-naturalists of the 1850's performed invaluable service for natural history in general and for ornithology in particular, by contributing to the Pacific Railroad Survey Report. Baird, as Assistant Secretary of the Smithsonian Institution, inspired most of this work. As official naturalist to the Pacific Railroad Survey, he requested the assistance of the young, well-educated army surgeons, who, as a matter of policy, were sent West for duty after receiving their commissions. This "first generation" includes a number of well-known names, such as James Graham Cooper, George Suckley, Caleb Burwell Rowan Kennerly, Adolphus Lewis Heermann, and Thomas

Charlton Henry, who accompanied the various surveys to the Pacific. Many others, such as Ebenezer Swift, John Fox Hammond, and Lewis A. Edwards were stationed at army posts in Arkansas, Texas, and California. Governor Isaac Ingalls Stevens, Director of the Survey, instructed the naturalists to keep daily journals of their observations. With the help of John Cassin and George N. Lawrence, Baird published a summary of these journals in the ninth volume of the "Pacific Railroad Report" in 1858 [*18*]. Two years later this work was republished with additions and corrections as "The Birds of North America."

Several of the surgeon-naturalists who worked in the West after the Civil War, including Elliott Coues, Edgar A. Mearns, and Robert Shufeldt, were involved in the establishment of the American Ornithologists' Union. Charles Emil Bendire, although not trained as a physician, was hospital steward early in his career and therefore the United States Army Medical Department also claimed him as one of its ornithologists [*18*]. Other active ornithologists, James Cushing Merrill and Samuel Moore Finley among them, stayed in the West during the 1880's, but sent extensive collections to the Smithsonian Institution.

A number of positions, then, were available throughout the 19th century for people engaged in ornithological investigation, but these posts also included other duties. This was equally true of curators in the several new museums established in the United States around the middle of the 19th century.

The Institutionalization of American Ornithology

In the United States, the establishment of a rigorous scientific method in ornithology, the formation of a central disciplinary association (the American Ornithologists' Union) and the initiation of its journal *(The Auk)* occurred in the last quarter of the 19th century. It was a part of the differentiation of science in America.

Two main factors led to the formation of the A.O.U. The first was the realization by many Americans that the seemingly endless frontier and its supply of wildlife were rapidly disappearing and that legislation and organizations were needed to protect them [*6*]. Not only had pioneer settlers, with their increasingly efficient firearms, reduced the once abundant wildlife out of sheer ignorance, but military and feminine fashions decimated several bird populations [*11*] through their incessant demand for feathers, wings, and even whole birds for hat decorations.

The second factor involved in the establishment of a national ornithological association was the question of nomenclature. During the 19th century, knowledge of the North American avifauna increased rapidly, due to the naturalist-ornithologists of the various government explorations, and also to the many individual naturalists, such as Alexander Wilson, Thomas Nuttall, Charles Lucien Bonaparte, John James Audubon, John Cassin, and others, who began publishing works on American birds. Books on economic ornithology and state bird books also began to appear. The increasing number of ornithological publications in which many of the newly discovered species were described and given scientific and vernacular names caused considerable nomenclatural confusion. A national ornithological society clearly was needed to deal with these and other problems [*1*].

The Establishment of Ornithological Societies

The story of the founding of the American Ornithologists' Union has been well documented [*1, 7*]. It may not be known generally, however, that most of the founders of the A.O.U. were amateur ornithologists, who made their living in other occupations and professions (Table 1).The British Ornithologists' Union was proposed as model at the founding conference of 1883, where the participants designated four important areas of North American ornithology for study: classification and nomenclature, distribution, migration, and the status of the European House Sparrow in America.

According to the "Certificate of Incorporation," the objectives of the A.O.U. included "The advancement of its members in Ornithological Science; the publication of a journal of ornithology and other works relating to that science;" (Palmer, *in* [*25*]). The journal of the A.O.U. followed the style and format of *The Bulletin of the Nuttall Ornithological Club* and, in fact, was a continuation of it. The new publication received the name *The Auk* in preference to *American Ornithologist*, a name sought by some of the members. J. A. Allen, the first president of the A.O.U. and former editor of the *Bulletin*, became editor of the new journal.

Apart from *The Auk*, the first major publications of the A.O.U. was the *Code of Nomenclature and Classified Checklist of North American Birds* published in 1886. The Checklist was immediately accepted, but the Code remained controversial. This was caused by the introduction of trinomials, or subspecific names, for all species "as demanded by the discovery of certain facts of evolution made evident by the study of the avian fauna of a large continent, through the accumulation of material sufficient to show the progress of differentiation resulting from environment." [*1*]. Eventually American and European ornithologists accepted the trinomial designations, because the Linnean binomial system was found to be inflexible for the exigencies of modern ornithological and general zoological research.

Within ten years of the foundation of the first scientific association of American ornithologists, other societies were established. The Wilson Society was originally founded in 1888 as the Wilson Ornithological Chapter of the Agassiz Association of the Middle West. Its journal was named *The Wilson Bulletin* [*22*]. The original Cooper Club (now the Cooper Ornithological Society) was organized in Santa Clara, California during the winter of 1890/1891, but it lasted only a short while. In 1893, Chester Barlow, a young amateur, organized the Northern Division of the Cooper Ornithological Club in San José. Later in the same year, a Southern Division was formed in Los Angeles. The two divisions held separate outings and conferences until 1926 [*30*]. After several attempts, the club established a satisfactory publication in 1899, the *Bulletin of the Cooper Ornithological Club*. In 1900 its name was changed to *The Condor*. The club's monograph series entitled *Pacific Coast Avifauna* (now called *Studies in Avian Biology*) was inaugurated the same year with the publication of Joseph Grinnell's "Birds of the Kotzebue Region, Alaska," based on his observations while panning for gold [*13*].

The establishment of these and other ornithological societies brought American ornithology a step closer to becoming a full-fledged discipline. There were also an increasing number of paid positions for ornithologists. Museums needed larger staffs for curatorial duties, and an increased interest in economic ornithology opened up paid positions in various state departments. The Division of Economic Ornithology and Mammalogy of

TABLE 1

The Founders of the American Ornithologists' Union (1883)

Name	*Occupation*	*Contributions to ornithology*
Allen, Joel A.	Assistant in Ornithology, M.C.Z.	Geographic distribution, nomenclature, prolific author
Aldrich, Charles	Businessman	Protection of birds (Iowa Law, 1870)
Bailey, Harry B.	Businessman	Regional ornithology, collection, oology
Baird, Spencer F.	Secretary, Smithsonian Institution	Collector, field ornithologist, systematist
Batchelder, Charles	Businessman	Collector, regional ornithology
Bendire, Charles E.	Army officer	Oology, honorary curator of Dept. of Oology, U.S. National Museum; started "Life History" series
Bicknell, Eugene P.	Businessman	Bird song, regional ornithology, active on committees on Migration of Birds, House Sparrow, Bird Protection
Brewster, William	Wealthy amateur	Water birds, bird migration; first to repeatedly study birds of a certain region
Brown, Nathan C.	Wealthy amateur	Regional bird study, collections, on committee on Status of House Sparrow
Chamberlain, Montague	Businessman	Birds of Canada, New Brunswick; revised Nuttall's Manual
Cory, Charles B.	Wealthy amateur	Expert of birds of Florida, West Indies
Coues, Elliott	Secretary and naturalist to Geological & Geographical Survey of Territories	All around ornithologist; taxonomy, life histories, nomenclature, classification
Elliot, Daniel G.	Wealthy amateur	Monographic studies of certain species or families of birds, good illustrator
Fisher, Albert K.	Physician	Bird protection, member of committee on Migration and Distribution of Birds
Henshaw, Henry W.	Civil servant in Bureau of American Ethnology	A leading field ornithologist, member of committee on nomenclature of birds
Holder, Joseph B.	Surgeon, U.S. Army	Collections, flights of birds
Lawrence, George N.	Retired businessman	Expert on birds of tropical America
Mearns, Edgar A.	Surgeon, U.S. Army	Collections, regional ornithology, assistant curator A.M.N.H.
McIlwraith, Thomas	Businessman	Birds of Ontario, member of Committee on Migration of Birds
Merriam, C. Hart	Physician	Distribution of birds, chief of committee on Migration of Birds

TABLE 1

The Founders of the American Ornithologists' Union (1883)

Name	*Occupation*	*Contributions to ornithology*
Prentiss, Daniel W.	Physician, Professor of Medicine	Birds of District of Columbia, co-authored with Coues
Purdie, Henry A.	Businessman	Birds of New England, birds' eggs and nests
Ridgway, Robert	Curator of Birds, Smithsonian Institution	Systematist, bird artist, A.O.U. checklist committee
Shufeldt, Robert W.	Surgeon, U.S. Army, Curator Army Medical Museum	Osteology of birds, palaeo-ornithology, pioneer of bird photography
Wheaton, John M.	Physician, Professor of Anatomy	Regional ornithology (Birds of Ohio)

the United States Department of Agriculture was founded in early 1885. C. Hart Merriam left medical practice to become its director and soon persuaded another physician, A. K. Fisher, to give up medical practice to become his assistant. Their aim was to study in depth the relationships of birds to agriculture [*11*].

The Beginnings of Ornithological Education

The late 19th century ornithologists were still self-educated specialists. Training and certification at the university level were not achieved until shortly before World War One. Biology as a career became more popular by the end of the last century and training for it was freed from its traditional ties with the medical faculties. The first college course in ornithology began in 1895 at Oberlin College under the leadership of Lynds Jones [*20*]. A widespread interest in ornithology around this time gave rise to several summer courses in various locations, such as the Woods Hole Marine Laboratory in Massachusetts and the Hopkins Seaside Laboratory in California, where Grinnell, then an undergraduate at Stanford University, taught ornithology during 1901 and 1902. In the summer of 1909 he began ornithology lectures at the University of California, Berkeley. William T. Shaw gave summer courses in bird life at the Marine Biological Station at Olga, Washington from 1909 to 1911 and started to lecture at the State College of Washington in 1912. At Cornell University, Ithaca, New York, Arthur A. Allen, a recent Ph.D., started lecturing in ornithology in 1911. Four years later he became the first assistant professor of ornithology in the United States. His first graduate student, Ludlow Griscom, became an authority on field identification. Griscom, before his graduation in 1915, also gave summer ornithology courses at the University of West Virginia. Thomas S. Roberts, a well-known Minnesota physician and professor of pediatrics, started to give a bird identification course at the University of Minnesota in 1915. This course, however, was never intended to train professional ornithologists [*5*]. From the second decade of the 20th century, the number of universities and colleges teaching ornithology increased sharply, producing a corresponding increase in positions for professors, lecturers, and assistants.

Amateurs and the Ornithological Literature

One of the ways of assessing the scientific output of any scientist is by evaluating his/her contribution to the "literature." Hagstrom [*16*] emphasized that in science, publishing manuscripts in scientific journals establishes the author's status as a scientist and assures him/her of acceptance within the scientific community.

To evaluate the contribution of amateurs to the ornithological literature of the 20th century, I analyzed selected volumes of *The Auk, The Wilson Bulletin,* and *The Condor* for authorship. I considered a professional ornithologist to be any person occupied with the scientific study of birds, having institutional affiliation with universities, museums, federal or state departments, or equivalent, and contributing to the science of ornithology by publishing the results of his/her research. I considered as amateur any author publishing in these journals but having no institutional affiliation or financial support for research from any official source. Although other publications are available, such as local, regional, and state publications, and some well-known national journals, the three journals associated with the major American ornithological societies have been published uninterruptedly since the end of the last century. This makes them particularly suitable for a study of the changing ratio of amateur authors to professional authors.

The analysis included all communications to these journals exclusive of book reviews, social notices, obituaries, and reports of meetings, conferences, and committee work. There is an expected decrease in the nonprofessional contributions as the century progressed (Table 2), paralleling the increasing professionalization of the field. At the same time, amateur authorship of 12 percent of all papers in 1975 is an important indication of their continued importance, considering that most other fields had virtually stopped publishing non-professional contributions by this time. In American ornithology, however, the 12 percent is just the tip of the iceberg, representing either unusual observations or lengthy study projects carried out by one or two individuals. It would be misleading, therefore, to ignore some of the other ways amateurs have contributed to ornithology over the past 100 years.

The Growth of Popular Interest

Over the last hundred years, a significantly greater number of nonprofessionals have contributed to ornithology. There have been several reasons for this development: (1) Birdwatching became a popular hobby, and many birders showed a serious interest in participating in the scientific study of birds. (2) The increasing number of local societies which followed the popularization of birdwatching were important in nature and conservation education and in organizing research projects. (3) Bird books became more numerous and less expensive. (4) Improved instrumentation contributed to easier and more efficient identification of birds. This was especially important, since in the 20th century the living bird and its habits replaced specimens as the focus of interest and study.

In 1901 Robert Ridgway "defined scientific ornithology as the identification and classification of birds, and he defined field ornithology as the collecting and stuffing of specimens." [*14*]. The advance of modern field ornithology was greatly aided by better binoculars, telescopes, cameras, and portable tape-recorders, all of which helped to replace the shotgun.

In the early days of the American Ornithologists' Union, a great effort was made to involve people from all walks of life in contributing data for the work of the various committees. In response to an appeal by the Committee on Migration of Birds, much of the information was provided by amateurs and not by experienced ornithologists. C. H. Merriam, head of the committee, contacted 800 newspaper editors, who advertised circulars available to prospective observers, giving instructions as to the methods of observation and reporting. The "Instruction to Collaborators" also appeared in the first issue of *The Auk* in January 1884. Three months later there were 500 people engaged in observations and by the end of the year their number had risen to 650. One hundred of these were in Canada. Numerous lighthouse keepers also became engaged in bird observation. The groundwork had been done for involving a significant segment of the population in collecting data for ornithology.

Bird-banding emerged as one of the most important techniques in the study of the living bird. It became popular with the availability of lightweight aluminum bands around the time of World War One. Amateurs participated in banding activities from the beginning and have aided significantly bird-migration projects and life-history studies. Several American bird-banding associations were formed and the Northeastern association's journal, *Bird-banding*, is ranked among the important ornithological journals of the continent.

Amateurs participate in large numbers in providing data for the National Audubon Society's annual Christmas Count. When this activity was started in 1900 by Frank M. Chapman of the American Museum of Natural History, it had only 27 participants in 25 areas. In 1954, over 6,000 people spent a day counting birds in the field in 516 localities, each area consisting of a 15-mile-diameter circle [*9*]. By 1977 there were 1,200 count areas, with over 30,000 participants [*17*]. The data collected contributes information on roost location, species distribution, and changes in centers of populations [*23*]. *American Birds* (formerly *Audubon Field Notes*) is the sponsor of the Christmas Count, as well as other important projects that involve both professionals and amateurs all over North America. These are the Breeding

TABLE 2

The Percentage of Contributions by Amateur Authors to Three Major Ornithological Journals

Year	*The Auk*	*The Wilson Bulletin*	*The Condor*
1900	72	83	77
1910	75	84	79
1925	63	91	67
1950	47	46	34
1975	12	12	13

Bird Census and Winter Population Study, the Quarterly Field Reports, and the relatively new Blue List. Inaugurated in 1971, the Blue List attempts to alert ornithologists to decreases in bird populations that may presage a species being placed on the "endangered" list. The Quarterly Field Reports, contributed mostly by amateurs, cover each season more than twenty areas north of Mexico in a systematic way. These reports provide migration records, indicate increasing and decreasing population trends, and inform ornithologists of incursions and invasions of certain species. An increasing number of research projects are carried out with the data provided by these field reports.

A government institution capitalizing on amateur expertise is the United States Fish and Wildlife Service's Breeding Bird Survey. It was launched in 1965 in one area but expanded rapidly, and by 1968 it included much of the United States and Canada. The data culled from the Survey are included in a statistical analysis in which each physiogeographic region in each state and province is analyzed separately. The data are available to all ornithologists, professional and amateur, for the analysis of bird populations or for preparing environmental statements [*23*].

Modern Institutions of Amateur Involvement

There are numerous academic institutions in North America concerned with the training of teachers and researchers in ornithology. There are very few institutions, however, that encourage the collaboration of amateurs and professionals in the various research areas of bird study. One outstanding example is the Cornell Laboratory of Ornithology, which opened in 1957. Its role "has become one of collection, interpretation, evaluation and dissemination of information about birds to both amateur and professional ornithologists" [*23*]. Amateurs make valuable contributions to the Laboratory's Library of Natural Sounds, the North American Nest Record Card Program (NRCP), and the Colonial Bird Register (CBR). The CBR, a joint venture of the National Audubon Society and the Laboratory of Ornithology was organized in 1975 and serves as an important center for compilation and standardization of data collected by various agencies, such as the United States Fish and Wildlife Service. By the summer of 1979 it contained 6,500 records of visits to colonies. All the data have been computerized. The NRCP was started in 1965 and presently has nearly 264,000 cards on file, of which 52,000 are computerized. Amateurs contribute most of the nesting cards for this program.

Bird observatories have been in use for the study of bird migration and as centers of bird-banding in Europe since the end of the 19th century. In North America, where mist netting antedated the construction of Heligoland traps, bird-banding developed as an individual, rather than a collective, activity. Therefore, the concept of the bird observatory has not been exploited as extensively as in Europe [*28*]. There are several, however, that are worthy of mention since, like the Cornell Laboratory of Ornithology, they act as local centers of amateur involvement.

The Long Point Bird Observatory of Port Rowan, Ontario, was founded in 1960 and is the first station of its type in North America. The LPBO depends heavily on volunteers to carry out its research projects in cooperation with the professional staff. The Observatory's headquarters contain the research laboratory and a library. Two field stations provide facilities for monitoring migration and for bird-banding activities. A major project aims at determining the status of breeding birds at Long Point, some of which are rare or endangered species. LPBO sponsors the Ontario Bird Feeder Survey and the Great Lakes Beached Bird Survey. The Ontario Heronry Inventory is a joint project with the Canadian Wildlife Service and the Ontario Ministry of Natural Resources. An active educational program for schoolchildren and the training of volunteers in banding and other field techniques are among the other functions of the Observatory.

The Point Reyes Bird Observatory in California started in 1965 as a center for regular year-round programs of bird-banding in cooperation with the U.S. Fish and Wildlife Service. The PRBO is a "research organization which is virtually dependent upon volunteer help for its survival" ([*23*], p. 38). Long term research projects are an important part of the observatory's work. Some of the recent projects include a bird atlas of Marin County, intensive studies of the Snowy Plover *(Charadrius alexandrinus)* populations at various locations, shorebird censusing on Bolinas Lagoon and on other estuaries, and since January 1979, the Palomarin Landbird Ecology Project, which aims at recording changes in the avian community of the coastal sage scrub habitat at Palomarin Ranch. The PRBO, in cooperation with the U.S. Fish and Wildlife Service, also oversees the preservation of seabird colonies on the Farallon Islands, a major nesting site on the Pacific coast.

The Manomet Bird Observatory on the East Coast was founded in 1969 for reseach and education in environmental biology, especially the use of birds as environmental indicators. Long term research is an important function of the Observatory. Amateurs have widely participated in the various projects from the inception of this center, most of which involve bird-banding. Their most ambitious project to date is the International Shorebird Census, which is a cooperative project with the Canadian Wildlife Service. Another study "of autumnal shorebird distribution has grown to include 100 to 200 observers in ten New World nations and commonwealths. The survey was launched through personal contacts and announcements in the major ornithological journals. From the outset, it has relied upon volunteers" [*23*]. Operation Seawatch is a third major project, which records migrating waterfowl and other seabirds as they fly past certain selected coastal promontories.

Some Individual Contributors

Of the many independent studies that have been carried out by amateurs during the present century, the better known include Margaret Morse Nice's pioneering *Studies in the Life History of the Song Sparrow*, Lawrence Walkinshaw's study of the Sandhill Crane *(Grus canadensis)*, and Harold Mayfield's work on the Kirtland's Warbler *(Dendroica kirtlandii)*. There have been numerous other important projects, but only a few can be mentioned here. Alexander Skutch started ornithological research while employed as a botanist in South America and subsequently has published many works dealing with the bird life of the tropics. Frank B. Smithe, a mechanical engineer by training, is the author of *Birds of Tikal* and of the more recent *A Naturalist's Color Guide*. Louise de Kiriline Lawrence studied bird life around her home in Southern Ontario. One of her projects, entitled *A Comparative Life History Study of Four Species of Woodpeckers*, was published as an A.O.U. monograph. Crawford H. Greenewalt, a chemical engineer by training, published several important studies on hummingbirds, weight-wing ratio analyses of animals, and the physiology and mechanics of bird vocalizations. The latter was an especially important study for ornithologists in which Greenewalt used an interdisciplinary approach, including animal behavior, anatomy, physiology, physics, and accoustical and mechanical engineering [*15*]. Charles Hartshorne, a philosopher by profession, whose study of bird song took him to every continent, published *Born to Sing* in 1973. George B. Reynard, a botanist, conducted special studies on the vocalizations of rails, owls, and caprimulgids. The late Paul Schwartz was a mechanical engineer. Apart from amassing the largest collection of recordings of songs and calls of South American birds, his studies and publications added greatly to the understanding of the taxonomy and distribution of birds of northern South America.

Although bird artists have contributed to ornithology for hundreds of years, some of them in our own time have gone beyond the illustration and discovery of new species of birds. Roger Tory Peterson is well known as an artist and author of the first modern "Field Guide to the Birds of North America." It may not be generally known, as one professional expressed it, that "In . . . the tremendous rise of ecological and other field studies in ornithology over the past four decades . . . the Peterson field guides played a central role and thus contributed significantly to scientific ornithology." [*4*].

In a new project organized in 1977 by Paul L. Aird, a professor at the Faculty of Forestry and Landscape Architecture at the University of Toronto, teams of amateurs searched for Kirtland's Warblers across the jack pine *(Pinus banksiana)* belt of Southern Quebec and Ontario with encouraging success.

The Profession Takes Stock

The time has arrived for an assessment of the present state of American ornithology. The number of ornithologists has increased significantly during the last hundred years. Ornithological societies have proliferated in the United States and Canada from one, the Nuttall Club, in 1873 to more than 800 in 1978 [*27*]. Almost all of them issue monthly, quarterly, or annual publications and are in some way involved in ornithological education and conservation.

The importance of the amateur in ornithology is being increasingly recognized by the professionals. This has been emphasized by a recent study funded by the National Science Foundation and carried out by the A.O.U. from 1976 to 1978. The Workshop on a National Plan for Ornithology was essentially a thorough review of the profession. The main subject areas studied by separate panels were the role of the ornithological societies and the amateur ornithologists, ornithological education, publication resources, special data banks, systematic collections, and obtaining and using birds. The amateur or "avocational" ornithologist was defined as someone whose salary and career were essentially independent of his/her ornithological interests and studies [*21*]. From the information collected by questionnaires, the panel studying the amateurs learned that North American nonprofessional ornithologists are a well-educated group, with over 90 percent holding at least bachelor's degrees and one third doctorates, usually not in biology. Most of them have engaged in some ornithological research and 60 percent have published technical papers. Most amateurs showed interest in continuing their research efforts in ornithology. In terms of both quantity and quality of research contributions, amateurs are a major ornithological force to be appreciated and encouraged [*21*].

In February 1978, the National Audubon Society and the Cornell Laboratory of Ornithology organized a conference on the subject of the Amateur and North American Ornithology. Twenty-seven ornithologists, amateur and professional, met at the Cornell Labortory of Ornithology, an organization that has successfully formulated and carried out research projects with the cooperation of professional and amateur ornithologists. The discussion at the conference revolved around the various possibilities of increased amateur involvement in ornithology.

What is the present position of the non-professionals in American ornithology? What can be done in the future? Their importance to the science is acknowledged by some far-sighted professionals who realize that, given the limited expansion of the field for professional ornithologists and the limited funds available for scientific research, many of the important tasks of ornithology would remain unaccomplished without the increased assistance of amateurs. Since amateurs are contributing to ornithology in a variety of ways, from data gathering to sophisticated research, this assistance can be in many forms. Some amateurs do the work of unpaid technicians, while others submit their research for evaluation by their peers, as do professional ornithologists.

The second half of the 20th century has been called the era of "Big Science," that is, of big, expensive instruments and costly projects involving numerous scientists. Large-scale scientific activity is not the discovery of the present century, of course, since the large-scale scientific expeditions of the 18th and 19th centuries also qualify as big science. In our own century, however, big science has become the norm, especially in America. By the late 1960's reduced funding seriously threatened the research potential of a scientific community conditioned to think in terms of expensive apparatus and huge budgets. American ornithology is in an enviable position, as is British ornithology, since it is able to increase its projects without necessarily greatly augmenting the funds needed for research, simply by involving more amateur ornithologists.

Capitalizing on Amateur Involvement

A consideration of successful projects involving both professional and amateur ornithologists in Britain, Canada, and the United States shows that they have the following characteristics in common: well-formulated projects, clear guidelines, personal contact in attracting participants, and good feedback and acknowledgement. Personal contact seems to be the most important single factor in the initial stages of a project that depends on team organizers. The successful outcome of a project depends on whether it is thought out and presented as a cooperative project with the non-professional as full participant, or whether it creates the impression that the amateur is going to be exploited without being given full credit for his/her efforts. The attitude of some professionals seeking amateur assistance seems to indicate that using the amateur in their projects is what they consider important. John M. McMeeking, representative of the British Trust for Ornithology, who attended the Audubon/Cornell Conference in 1978, said that "it must be seen that there is an amateur/professional team, and that amateurs are not being used as 'slaves' by professionals mainly concerned with advancing their own particular work" [*23*].

TABLE 3

A Typology of Amateur Involvement

Supporters	
Passive	Pay membership fees, but do not participate in activities
Active	Go to meetings, field trips, lectures, conferences; many are involved in conservation efforts; some are potential contributors or researchers
Contributors	
Organized:	
Infrequent	Irregular—provide sporadic data Regular—Christmas Count, Breeding Bird Survey
Frequent	Nest Record Card Program, Hawk Migration Watch, Beached Bird Surveys, studies involving banding
Independent:	
Occasional	Observations on bird behavior, distribution, and unusual occurrences
Regular	Quarterly field reports, nesting data
Researchers	Able to formulate and carry out independent studies on various aspects of ornithology

Scientific activity in ornithology in addition to full-time work in other employment will have to be intellectually challenging and satisfying to entice many non-professionals to work on their weekends and their vacations. An increased awareness on the part of the professional group regarding the mechanism of collaboration with amateurs is an important requirement for augmenting their involvement in ornithological research. In formulating new research projects with amateur collaborators in mind, the already established activities of the amateur will have to be taken into account. Cooperation should be incidental and supplementary to existing interests. Furthermore, a project should have a discreet beginning and end, as few people can sustain their enthusiasm for a task that goes on forever (Mayfield *in* [*23*]).

Amateur ornithologists do not all have the same interest and potential for research. Considering their activities and the extent of their involvement, a typology of amateurs can be set up (Table 3).

The dividing lines between these groups are not rigid and there is some mobility from one section to another. Supporters constitute the largest group. It has been estimated that there are approximately 11.5 million birdwatchers in North America. Most of them belong to some nature-oriented organization. Contributors constitute the largest number of collaborators. With appropriate education and clear-cut guidelines, many supporters could be persuaded to contribute to ornithology. Researchers form the smallest group; they publish or attempt to communicate their results to the same peer review group as do professionals. Some independent contributors are potential researchers, given proper encouragement and training.

To increase the number of contributors and researchers, prospective organizers of cooperative projects should study carefully the *Directory to Cooperative Naturalists' Projects in Ontario—A Guide for Volunteers* [*19*]. This excellent publication by the Long Point Bird Observatory gives information on projects in Ontario that need volunteer help during the year. It describes the aims and volunteer requirements of each project and provides the names of contacts and organizers. The great variety of programs, such as seasonal studies, year-round studies, checklists, etc., provide scope for ornithological undertakings of various kinds and duration. Thus amateurs can choose one or more that suit their interests, abilities, and lifestyles.

A similar publication for the United States and the whole of Canada would provide the initial step in ensuring the future collaboration of many capable amateurs. At the moment there is no organization, similar to the British Trust for Ornithology, with the people to initiate it. Whether the National Audubon Society will take it up, or whether an American Trust for Ornithology would fulfill the need, remains to be seen. What is needed is positive action on the part of American ornithologists.

Conclusion

One may ask what the future holds for ornithology if the present efforts of many professional ornithologists succeed in integrating more amateurs into the activities of the science. Will they be regarded as vital participants of the science? Will they have more power in the running of the scientific associations in which, in the 1970's, they constitute half the membership? Increased amateur involvement is likely to augment their number in these "professional" associations. They will undoubtedly be given greater voting representation on councils, as they cease to be considered mere adjuncts to the professionals.

American ornithology has gone through several stages in its development, from being a part of natural history, to becoming a speciality in the late 19th century, and a scientific discipline by World War One. Now, it can be considered a transdisciplinary science, because it attracts scientists from many related fields. Who and what is an ornithologist? Until the beginning of the present century, this term was applied to any person dealing with birds, whether he/she studied their habits and distribution, collected them for museums or zoological gardens, or painted them for the equivalent of our coffee-table books. They all made their contributions to the science of ornithology. In our own time, evolutionists, population biologists, ecologists, ethologists, physiologists and others work in ornithology; many of them belong to the A.O.U. and/or other major ornithological societies and publish in their journals. So do many doctors, lawyers, teachers, homemakers, and business persons.

The 20th century verbal distinction between amateur and professional researchers in ornithology should be reassessed. Both groups contribute to the others' projects; they read the same technical literature and belong to the same associations. Both are members of the North American ornithological community. The continued non-professional involvement to date and the forecast of increased numbers of ornithologists who make their living in other fields sets this science apart from other sciences in America today. This must change the ideas of historians and sociologists of science regarding the constitution and functioning of professionalized scientific disciplines.

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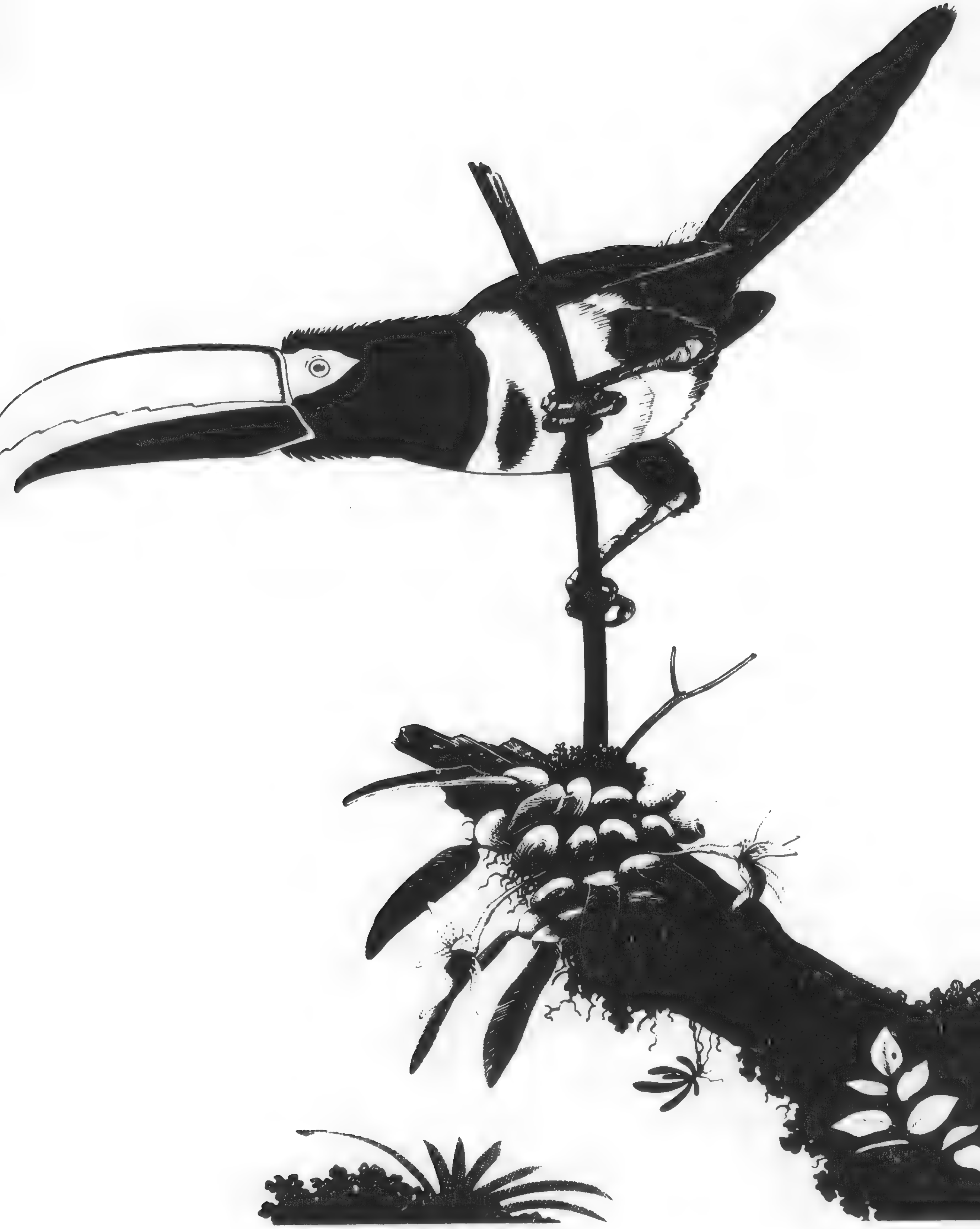


Fiery-billed Aracari, *Pteroglossus frantzii*. Painting by Dana Gardner.

GROUND BARBETS OF EAST AFRICA

LESTER L. SHORT and JENNIFER F. M. HORNE

Barbets are strictly tropical birds related to woodpeckers and toucans, and are noted for their bright colors and fruit-eating habits. Despite their colors, few species are well known because barbets generally frequent the tops of trees, where they are inconspicuous. The distribution of the 76 or so species includes tropical Asia, Africa, and the Americas, but they are most numerous and diverse in the forests, woodlands, and savannas of Africa. Perhaps the most unusual of the barbets are the three species of ground barbets (genus *Trachyphonus*) that occupy savannas and semi-desert of north-central, eastern, and southern Africa. Forsaking the treetop habitat of their ancestors, the ground barbets forage on the ground and in scattered low bushes. Most barbets nest in holes in trees, but some of the ground barbets burrow into termite mounds, or into the ground.

In eastern Africa we studied two of the ground barbets, the smaller D'Arnaud's Barbet *(Trachyphonus darnaudii)*, about six and one-half inches long, and the larger Red-and-yellow Barbet *(T. erythrocephalus)*, about eight and one-half inches long. Their interesting habits make these very vocal, conspicuous birds engaging subjects for study. Where they are not persecuted by humans, they become very tame, as at the game lodges and safari camps of various national parks and reserves of Kenya. Here they boldly seek food and may wander with abandon into one's cabin or tent, or inquiringly perch on one's foot or chair.

Plumage Patterns

The colors of these ground barbets are varied: brown or blackish spotted with white and otherwise marked with black and white, yellow, orange, or red. Although the birds are well marked and conspicuous from the front, their colors, and particularly the pale spotting, actually afford protective coloration. When one of the barbets perches in low bushes, or even on the ground, the intense African sun pales its overall color, casting the spots as a dappling that breaks up the bird's form and silhouette. This dappling effect especially obscures the tail, which is brown or black with half-moon-shaped spots lining its edges. The sunlight on the tail spots breaks up the shape of the tail, rendering it like an irregular stick, and thus obscuring the bird's form (since the tail protruding from an egg-shape characterizes a bird as such) from both observer and potential predator.

Range and Habitat

The range of D'Arnaud's Barbet extends from southern Sudan, southern Ethiopia, and Somalia southward through Uganda and Kenya to central Tanzania. It frequents scrubby, bushy savanna country and rather open semi-deserts at elevations up to 6,000 feet. The Red-and-yellow Barbet occurs from southeastern Sudan, southern Ethiopia, and Somalia south and east through northern Uganda and Kenya to northeastern Tanzania. Its habitat is much like that of D'Arnaud's Barbet, but it requires stream beds or termite mounds or irregular topography. Where both occur together, the Red-and-yellow Barbet usually is found in taller, denser vegetation and D'Arnaud's in more open terrain. Both species have well marked subspecies.

In contrast to the D'Arnaud's Barbet, which occurs in pairs or small family parties, the Red-and-yellow Barbet more often is observed in families and even in larger groups of up to eight or ten birds.

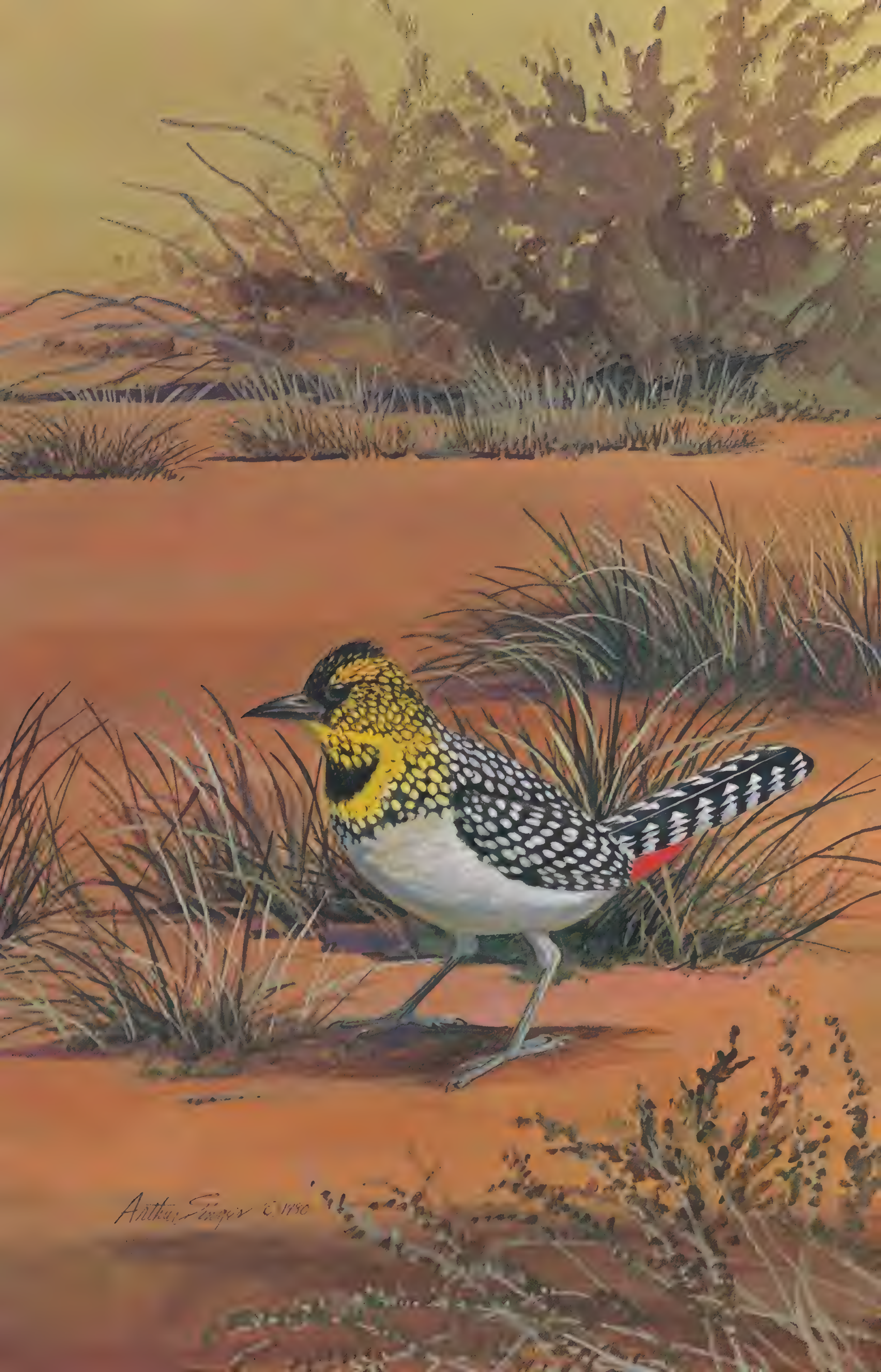
Food and Feeding

Although the ground barbets eat fruit, they also take many ants, termites, grasshoppers, and other insects on the ground, where the birds hop about in quest of food. When foraging in a group they render many low interactive *put*, chatter, and *chowk* notes. Their diet is varied and ground barbets are in fact omnivores; a group of three adult and five young Red-and-yellow Barbets studied at Olorgesailie Prehistoric Site south of Nairobi, although favoring particular items, sampled every kind of food we could conceive of giving them. They especially liked bits of raw ground beef (hamburger), and clustered about at our feet awaiting more. They also relished bacon rind, meat fat, flakes of cereal, cookies, pieces of mango, paw paw, banana, melon, tomato, potato, peanut butter, and bread and honey or bread alone. The aggressive Red-and-yellow Barbets drove away other would-be banqueters, even fending off the much larger ground squirrels that scampered about. One night, thinking to attract mammalian scavengers, we put some well-chewed lamb bones, dinner's aftermath, out in the grass beside our cabin. The next morning the eight Red-and-yellow Barbets were vigorously pecking away at the bones, even carrying them about as each bird sought to make off with one, and fighting among themselves for possession of a bone that was dropped. It was comical to watch one of these barbets hopping about with a bone in its bill nearly as large as the bird itself.

Their industry at feeding is exemplified by several actions of the Red-and-yellow Barbets. Frequently they hopped into the circular grass-walled and grass-thatched bungalow (in Africa termed "rondaval") as we sat outside. Within the rondaval they investigated clothing, pecked at shiny objects (field glasses, for instance), hopped about under the bed peering upward at it as if for insects, and generally climbed about the furniture. They also searched the edge of the floor, pecking into the adjacent grass wall, and worked over the grass thatch of the roof. Indeed they methodically investigated the outside of all rondavals and outhouses, searching every nook and cranny for insects seeking refuge therein. Sometimes they were "flycatchers," pursuing and seizing flying insects that they spied from their perch. Often they foraged in twos, advantageous in that an insect flushed by one bird could be seized by the other. Most amusing was their habit, doubtless learned from many experiences with automobiles, of carefully working over the wheels, grill, and underside, finding all manner of dead, dried insects and occasionally other animals. As they foraged they were very confiding; one could walk up to them, receiving only a glance as they continued feeding right at one's feet.

One dead Red-and-yellow Barbet, picked up from a road where it had been hit by a car, contained within its stomach the entire, if partly decom-

Plate 1. D'Arnaud's Barbet, *Trachyphonus darnaudii usambiro*. Painting by Arthur Singer.


Arthur Singer © 1980

posed, full leg (femur to toes) of a small bird. Barbets are not known to be carnivorous, and we cannot say whether the bird at least partly eaten had been found dead by the barbet, or had been caught, perhaps in its nest as a young bird, and then killed and eaten by the barbet. We did see Red-and-yellow Barbets chase small lizards, but they were unsuccessful in catching them during our observations. It is worth noting that in the American tropics, toucans, close relatives of the barbets, sometimes pull young birds from nests and eat them. Hence it is not unlikely that some barbets occasionally may feed on small lizards, birds, bird eggs, and perhaps small mammals.

Sociality

The ground barbets are social. Pairs remain together all year, and young birds associate with their parents for a long time; one or more of the young may accompany the parents through the next breeding season, helping them to raise that year's brood. Adult Red-and-yellow Barbets give a chucking call when food is found, and young that have left the nest quickly come to the food source, begging loudly and belligerently, driving back siblings, usually by means of displays such as crest-raising and fluffing of the plumage. Both parents and adult helpers, if present, feed the young. When Red-and-yellow Barbets are fed by humans, the adult female may, when the young birds are well-grown, join them in begging from her mate, and indeed she may snatch food from the bill of the juveniles as the adult male attempts to place it in the bill of the youngsters. Very young D'Arnaud's Barbets generally perch in a dense bush near the nest, calling in a low voice as the adults, one by one, feed them. On some cool mornings the youngsters may elect to stay in the ground nest and adults carrying food, after looking about for their offspring, are forced to re-enter the hole to feed them.

The behavior of ground barbets is marked by an engaging self-assurance; they are, in the absence of predators and disturbance, assertive and they tend to dominate other small birds. They utter many vocalizations, some of which serve to establish or maintain contact.

Nests

Red-and-yellow Barbets excavate nesting and roosting holes in the earth walls of ravines, where they are relatively safe from most predators but not from humans—some Africans dig out the nests, kill the adults, and use the feathers for adornment. Occasionally the holes are excavated in tall termite mounds. Eight birds at the Olorgesailie site had rather secure and exclusive holes, five in number, excavated into the side wall of an archeological site that is roofed over and is viewed by numbers of human visitors daily. We saw many roosting or nesting holes of other groups of this barbet in walls of neighboring ravines.

In contrast, D'Arnaud's Barbets excavate cavities straight down into open, essentially flat ground. Usually, the entrance is semi-concealed in the base of a shrub or tuft of grass. The excavated tunnel goes down for 20 to 36 inches or so, then turns to one side, expanding into an enlarged chamber used for roosting and nesting. There is but one entrance that serves also as an exit, posing a problem when mammalian or snake predators are about. D'Arnaud's is the only barbet to dig its nest vertically into flat terrain. It is a startling experience to discover the nest when a barbet suddenly bursts from open ground where no living animal is in sight. The Red-and-yellow Barbet's close relative, the Yellow-throated Barbet *(Trachyphonus margaritatus)* of the arid eastern Sahel (Lake Chad and Sudan to Somalia) also excavates into walls of ravines. Of the other members of the genus *Trachyphonus*, the Crested Barbet *(T. vaillantii)* of southern Africa forages on the ground and usually nests in holes in trees; and the forest-dwelling Yellow-billed Barbet *(T. purpuratus)* of western Africa to Zaire and western Kenya forages entirely in the understory of the forest and also nests in tree cavities. The mixture of terrestrial and arboreal habits in this genus of barbets is matched by that of the flickers, genus *Colaptes* (Nat. Hist., vol. 80, no. 3, pp. 66–74, 1971).

Defense

The Red-and-yellow Barbet gives a special rattling call when threatened by a snake or other terrestrial predator such as a mongoose. This call attracts the other members of a group, which rush in quickly, and it secondarily warns all animals in the vicinity. The barbets then maintain a ceaseless vigil, calling intermittently, flying and swooping over the predator, and following it through their territory. Other birds such as warblers and flycatchers join in, and the noise and general commotion accompany the predator as it moves about, until it leaves the area. Thus, the barbets serve as sentinels and watchdogs in their home area.

When feeding, they dominate other small birds, as noted above, even including flocks of aggressive starlings from which they staunchly defend their source of food, refusing to give ground unless completely outnumbered and attacked from several points at once. Even at that, we saw six or seven Superb Glossy Starlings *(Spreo superbus)* converge on a crouching D'Arnaud's Barbet and attack in a flurry. In the aftermath, the barbet spread flat out on the ground with one or two starling feathers in its bill, rose and continued its feeding as the starlings dispersed.

Duetting

Perhaps most appealing and unusual to human observers are the vocal and display antics of these barbets, pairs of which maintain their territories throughout the year. The adults, and to some degree the young birds, take part in duetting choruses of ringing, rollicking notes, a *ka-chow-ka-chee, ka-chow-ka-chee* (Red-and-yellow Barbet) or *ker-ta-tee-tootle, ker-ta-tee-tootle* (D'Arnaud's Barbet) that are among the most conspicuous sounds of the habitats that they occupy. The duet song is heard throughout the year, but no one so far has studied these birds year-round in any one location to determine the amount and intensity of singing, and the factors that affect the rate of singing. In fact the exact function of the duet song is not fully clear. It is apparent that: (1) these barbets sing the duet song all year; (2) both sexes participate in the duet song; (3) in both species the duet sets usually ascribed to the male seem fixed in pattern whereas the partner tends to fit its sets (usually ascribed to the female) to the "male's" song; (4) young birds or helpers may join in the Red-and-yellow Barbet's duets, and usually do not do so in the D'Arnaud's Barbets; but they are able to step in and duet if one of the pair disappears; (5) a duet tends to stimulate adjacent pairs to approach and begin duetting; (6) the approach of a barbet, or hearing a distant pair duetting, will intensify the duet or elicit a duet response; and (7) although the barbets have many other vocalizations (calls), they have no song, as such, other than their duet song. The intricate nature of the duet song and participation in it by both members of a pair indicate that it has some relation to reproductive synchrony. This is important in birds that breed seasonally in an equatorial environment where they maintain their territory all year. There is evidence that breeding follows the onset of rains, and the intricate duet song could play a role in synchronizing the breeding readiness of both members of a pair. Strong reactions of pairs to playback of duet songs, duetting "battles" between adjoining pairs at the common border of their territories, and year-round duetting suggest strongly that the duet songs also function in territorial defense and maintenance.

Shortly after daybreak Red-and-yellow Barbets exit one by one from their holes, giving low, chucking, interactive notes. They perch on a nearby bush and preen for a few minutes. Then, either in response to the morning's initial duet by some other, distant barbet group, or at the initiation of one of the adults, the group's first duet song is under way. A rattling call often precedes the duet as the primary adult male moves to a position high in a bush. As he starts calling, the adult female quickly takes up a position facing him or along side him. At least some of the other birds gather about them, occupying perches below the adults. As the young approach, they call *hik-ki-ik-ik* and sometimes giving chucking notes. Interactions occur when two birds pass close by each other. The youngsters often enter into the duet or one or two of them may "sit out" the duet, remaining perched or preening nearby; but they seem to join and quit it intermittently, never singing fully through the duet. However, the entry of a young bird into the duet at a point when it is tapering off may trigger a louder, stronger continuation of the duet by the adults. Also, distant duets affect the group's duet, spurring the birds to continue, or if they have ceased, triggering another duet. The male's notes are distinct, a *chow-chowp* or *ka-boop*, as are the more mechanical notes of the females, a *tit-tit-tit* that typically alternates with the male's notes to form the full duet song; the birds almost seem to utter their name, *red-and-yell-oh, red-and-yell-oh*. Females sometimes initiate a duet by giving a rattle call. The synchronous singing of three, four, five, or even more individuals makes it very difficult to analyze the duet songs that we recorded. We are studying ways to establish what notes each sex of young barbets utters, whether they are like the sexually distinct notes of the adults or not. Also, there are very faint pre-duet notes that usually are not heard at a distance, and therefore can be recorded on tape only under ideal conditions. These notes seem distinct for the two sexes, forming a faint but possibly very important pre-duet duet. We are investigating the structure and function of these pre-duet notes.

Duets of D'Arnaud's Barbets are shorter than those of the Red-and-yellow Barbet, usually 20 to 50 seconds in duration compared with the 40 to 100 or more seconds of most duets of the Red-and-yellow Barbet. Both species utter short, seemingly incomplete duets at times when they are disturbed or when interrupted by duets of other pairs, but we do not know whether this apparent difference is real, or if it relates to seasonal or other variation between the two species, perhaps at different stages of their life cycles. The D'Arnaud's duets that we have heard almost always involve the two adults of a pair; rarely does a third adult or a young bird join (or is allowed to join) to any degree in the duetting. Often there are extra birds, up to five in non-breeding groups but usually only one or two, associated with the primary pair. These mainly or entirely are the previous season's young. Such individuals may react first to playback, their strident chip notes helping to bring in the adult pair. It is easy to elicit a duet by playing back a brief portion of a recorded duet. In fact, if only one bird is attracted to the recording, at times it is possible to play back solo "duets" of the opposite sex, stimulating the single bird to respond. This response is exact, i.e., one can turn the tape recorder on and off, playing one, two, or more duet sets of the opposite sex, and the bird will join in, stopping as the recordist stops, starting on cue, and behaving in a "puppet-on-a-string" fashion.

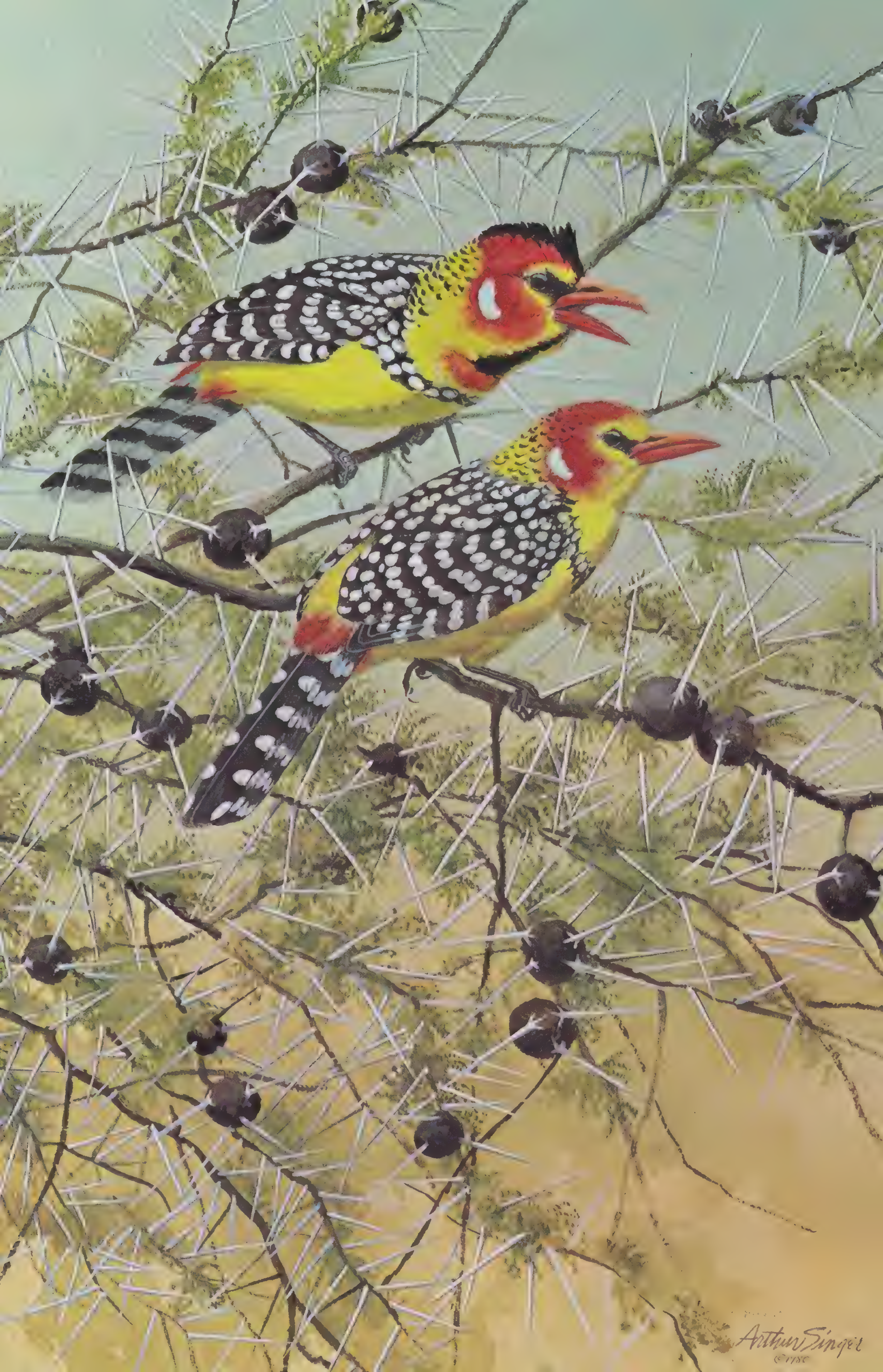
The barbets react strongly to conspecific duet songs, whatever their source. And all of the strongly marked subspecies of D'Arnaud's Barbets react to each others' songs. We should note that playback has its pitfalls. Responsive barbets may react interspecifically even to songs or calls of distantly related barbets, and we have observed many instances of not only other species of barbets, but of woodpeckers such as the Cardinal Woodpecker *(Dendropicos fuscescens)*, reacting vocally to barbet calls. There apparently is a tonal quality or some other parameter of the songs and calls of barbets and woodpeckers that renders them similar. Parenthetically, honeyguides, which also are piciforms, also respond to duetting barbets of some species (Short and Horne, Amer. Mus. Novitates, no. 2684, 1979), although this probably serves in some way to further their parasitism on barbets and woodpeckers.

In Red-and-yellow Barbet duets, songs are initiated by either sex, although the male does so more often. It usually is the male that reacts to a distant conspecific duet by ceasing its other activities and hopping or flying to a vantage point to look about. He then may utter several notes, which seem to bring his mate "on the double." She joins in, supplying sharp *tick* and *tee* notes to accompany his more mellow and longer tootling notes. That the notes are not absolutely sexually fixed in D'Arnaud's Barbet is indicated by instances in which a male utters the "female" part, and vice versa. Removal of one of a pair results immediately in its replacement in the duetting pair by another barbet of the group, presumably a young one, which commences to duet. The new duetting partners often have difficulties meshing their respective parts. When both members of a pair are removed, two of the other barbets in the social unit immediately form a new duetting pair, although the duet is not as complete or properly timed as in the original pair.

Display Accompanying Duetting

Accompanying the loud duet song are displays that relate to the status and sex of the participating individuals. The dominant male, presumably the paired male of the Red-and-yellow Barbet, initially may cock his tail as he begins to duet. He quickly hops up to a vantage point on a bush, tree, building, or other suitable place. As his mate joins him and he starts to sing he raises his crest, erects the feathers on the sides of the head, puffs out his throat, fluffs his rump and undertail feathers, raises his tail over his back or holds it downward and pumps it slightly, and quivers his wings. Feathers of all of the body areas involved in these displays are distinctly marked,and they are positioned to show off their colors. Thus, the male's black crown and throat patch are erected, the white and black ear patch stands out against surrounding red feathers, the fluffed red rump feathers are exhibited, and the spots and bars of the slightly moving tail and wings are rendered conspicuous. The fluffed appearance of the displaying bird is in strong contrast to its usual slim posture. The female of the pair may face her mate, or may perch beside him. Her displays are similar to those of the male but she

Plate 2. Red-and-yellow Barbet, *Trachyphonus erythrocephalus*. Painting by Arthur Singer.


Arthur Singer
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always holds her tail downward and her puffed throat, lacking the black mark, and her erect red crown clearly indicate her sex.

Other individuals participating in the duet, whether adult or immature, perch below or to one side of the pair, none of them taking a higher position or a place between or very close to the members of the pair. These other participants may display much like the pair, but they show fewer, less intense displays because they display only when singing; and they join and drop out of the duet intermittently and usually are silent during most of the duet. Thus, their behavior and their position to one side or below the pair contrasts strongly with those of the primary birds, or pair, that maintain their prominent position and vocalize more or less throughout the duet. They also tend to display even if they chance to cease duetting momentarily. Since secondary birds sporadically enter and leave the duet display, there may be two birds displaying and singing at one moment, four the next, then more or fewer a few seconds later. The greatest number of birds participate at the start of the duet. A duet display may seem about to terminate, or actually cease, only to begin with renewed vigor whenever a member of the group happens to fly in, announcing its arrival with a rattling call.

The sexes of D'Arnaud's Barbets, unlike those of the Red-and-yellow, are alike in plumage, and not surprisingly their display postures are to an extent different. In full display both sexes show a fluffed plumage and erect crest. A head-on view of the barbet in display shows an almost owl-like appearance of the head except that the eyes are obscured by the feather spotting. As the duet song begins and the female's location is evident to the male, in most cases he lowers his tail and begins to flick it in time with his utterances. However, the male occasionally raises his tail over his back in the usual manner of the female. His crest is erect, as are most body feathers, especially the red undertail coverts. He may face the female, then turn away from her, or both birds will face toward the direction of a distant duetting pair. In high intensity displaying, the female usually cocks her tail far forward over her back, spreading her tail feathers, and flicks it both from side-to-side and up-and-down somewhat; simultaneously she quivers her wings. From the front her tail swings rapidly back and forth over the head and crest, displaying the tail barring in a dizzying blurred movement. From the rear the red "powderpuff" of undertail feathers is rendered more conspicuous by the rapidly moving, barred tail, movements of which focus the onlooker's attention on the red undertail coverts. She may face the male, then turn about, presenting her rear with tail and red undertail "flashing" toward him. The female tends to move about more than the male does. Her crest seems less erected than that of the male. Both sexes have a curiously hunched posture, the fluffed head and neck feathers accenting this appearance, and to the rear the erect feathers at the base of the tail project, apron-like. The postures of both male and female bear some resemblance to avian soliciting postures, and there also are similarities to postures of begging juvenile barbets.

We stress that at times both birds of a duetting pair of D'Arnaud's Barbets may hold the tail downward as they duet. Although we are in the process of studying this situation further we can report that: (1) the songs and display posture and movements of the tail are not absolutely specific to the sexes; for example, a duetting bird with the tail up may utter the male duet song, and can be a male, and *vice versa*; (2) young birds accompanying a pair do not duet until something happens to one of the adults, in which case a young bird (or "helper" bird) will step in immediately and commence duetting with the remaining primary (adult) barbet; and (3) we have recorded on tape a number of "solo" duet songs, usually of one individual, but not always the male. This information suggests that the displaying sexes cannot be determined with certainty on the basis of the song-type or display-form.

In D'Arnaud's Barbets, the presence of a third, usually young bird accompanying the adults (there may be as many as five just after breeding) may interfere with the duetting. It is safe to say that any barbet flying to the display site will disrupt the duet display. Participation in the duet by a third individual is rare, much more so than in the Red-and-yellow Barbet; and the vocalizing of the third bird, if any, is half-hearted, usually one or two notes, and with no or little display. However, as we noted above, removal of one of the pair results in almost instant replacement of the lost bird by one of the several presumed young birds in a group.

Many questions remain to be answered about these lively and charming birds. The functions and seasonal variations of their duet songs, the development of vocalizations in young barbets, the nature of the sexual differences in vocalizations, the differences among the more and less terrestrial members of the genus, the nature of formation and breakup of the barbet groups, and the efficacy of geographical vocal differences in preventing interbreeding among races of D'Arnaud's Barbets are only some of the problems that remain to be investigated, and we are continuing our studies in some of these directions.

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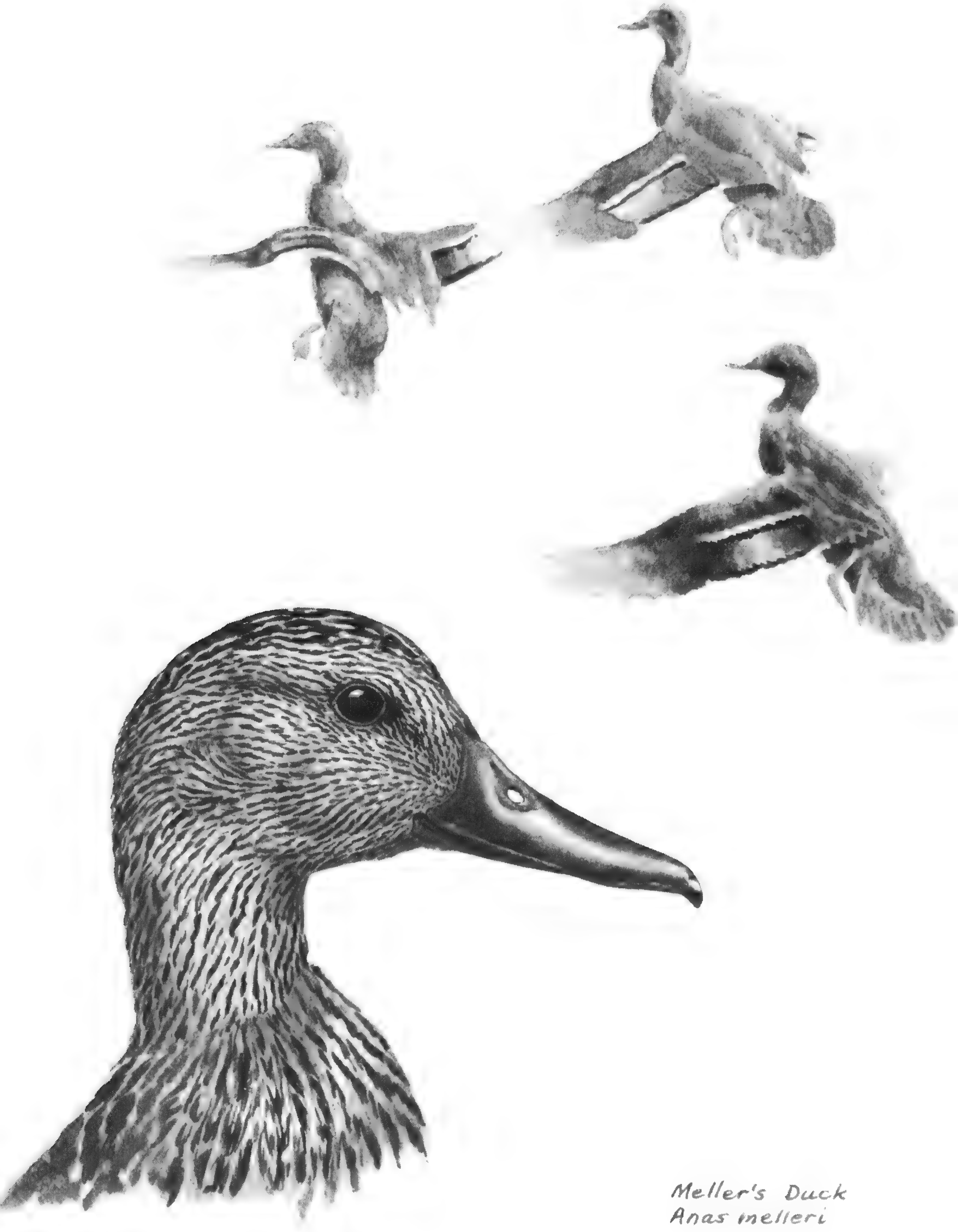
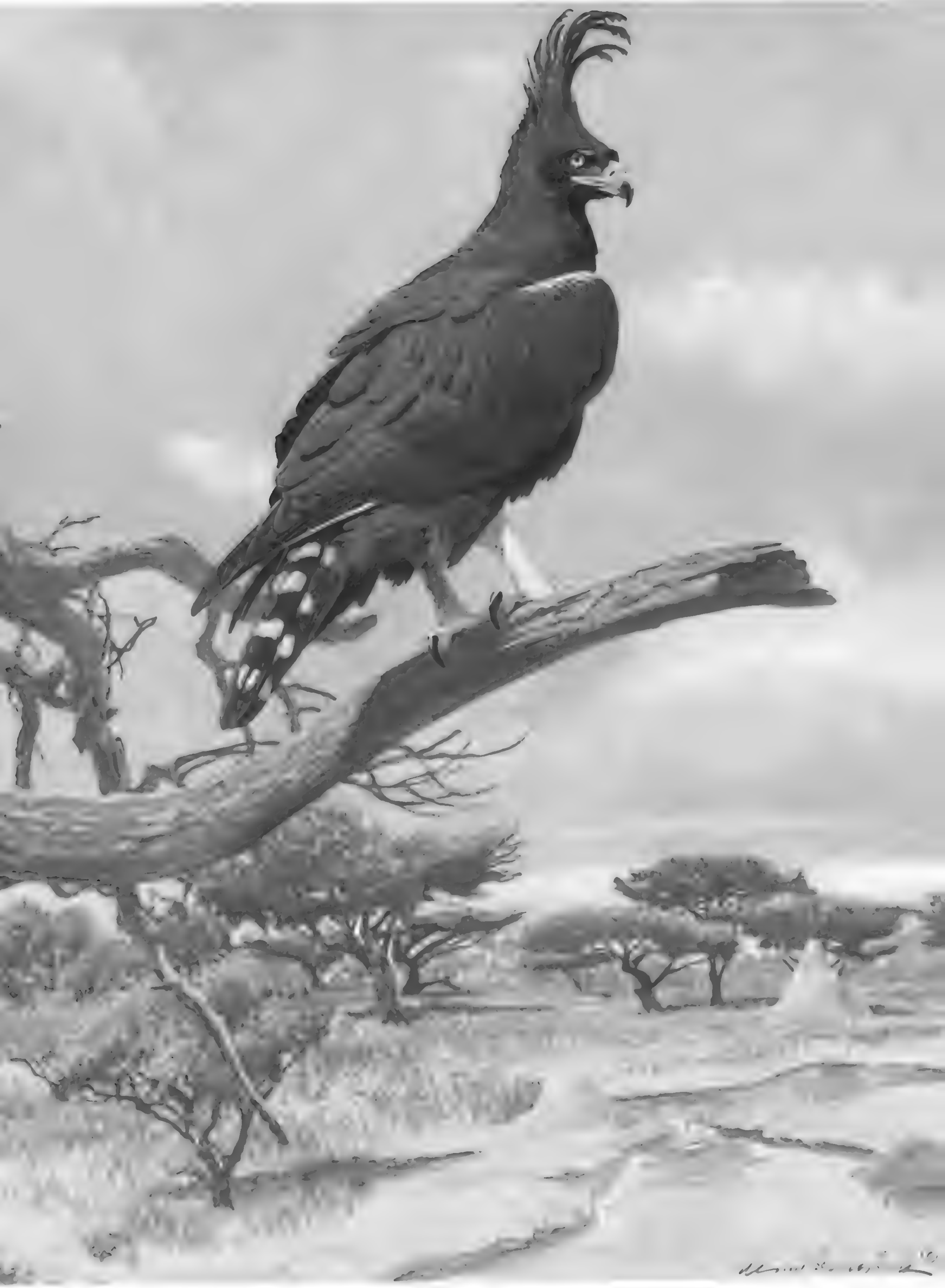

Meller's Duck
Anas melleri

Meller's Duck, *Anas melleri*. Painting by Terence Shortt.



Long-crested Eagle, *Lophaetus occipitalis*. Painting by Donald Leo Malick.

SWINHOE'S PHEASANT IN TAIWAN

SHELDON R. SEVERINGHAUS

Swinhoe's Pheasant *(Lophura swinhoii)* occurs only on the island of Taiwan (Formosa), about 160 kilometers off the coast of mainland China. The species was described by Gould [*7*] and named after Robert Swinhoe, the British diplomat who obtained the first specimens.

Since 1862, only two ornithologists have seen Swinhoe's Pheasant in the wild and published their observations: Goodfellow in 1906 [*14*] and Wayre in 1967 [*24*]. Swinhoe himself knew the species only through specimens taken by collectors. This pheasant has been considered rare since its discovery [*19, 26*] and is listed as an endangered species [*6, 9*].

From 1972 to 1974, I surveyed Swinhoe's Pheasants in the wild. This report focuses on the status, distribution, ecology, and behavior of Swinhoe's Pheasant as evaluated in 1974 on the basis of the two-year survey.

Methods

A field team of four people made 34 trips into the mountains, covering 7,000 km (2,000 km on foot). For each sighting of wild Swinhoe's Pheasants, we systematically collected data on location, habitat, and behavior. We interviewed several hundred people about the pheasants, including members of the island's nine aboriginal tribes. Colored paintings of the male and female pheasants were shown to each person interviewed to assure that questioner and informer were talking about the same species. For reported sightings, we collected data on location, habitat, behavior, and additional anecdotal information on their natural history.

The team discovered an area, referred to as the Reserve, where conditions were excellent for sighting wild Swinhoe's Pheasants (Figure 2). It was set aside in 1974 as the Chu Yun Shan Nature Reserve by the Taiwan Forestry Bureau as a result of this study (Figure 5).

We did not trap, mark, and release wild pheasants because of the possibility of mortality to an endangered species and because the small chance of returns did not make the trapping time and effort worthwhile for this type of study.

Several terms are used frequently in this paper. *Party kilometers* refers to the number of kilometers walked by one team member alone or by two or more members together. *Party hours* refers to the number of field survey hours spent by one team member alone or by two or more members together. *Direct encounter* refers to the sighting or hearing of one pheasant alone or two or more together by the field team. The term "direct sighting" is used interchangeably. *Reported encounter* (or reported sighting) refers to reliable reports of pheasants having been seen, heard, or captured by people who were interviewed by the team.

In two years, the team had 58 direct encounters of wild Swinhoe's Pheasants and received 155 reported encounters. In this paper, I have used only those reported encounters which were supported by the date and place birds were seen or taken.

Distribution

Record of Pheasants

From 1862 through 1976, there have been a total of 335 records of Swinhoe's Pheasants at 146 localities (Figure 1). The present distribution of this species is diagrammed in Figure 3.

In 1903, LaTouche [*3*] noted that Swinhoe's Pheasant ranged almost the entire length of the island but appeared confined to the central chain of mountains. Although more specimens were collected in the ensuing years, this general description of the pheasant's distribution was maintained by later workers [*5, 21, 25*].

Direct and reported sightings from 1972 to 1976 indicated that Swinhoe's Pheasants were still widely distributed, although probably not at the southern tip of the island as reported by LaTouche [*11*] and Bianchi [*1*]. One hunter said Swinhoe's Pheasants were found in Kenting Park (Figure 1) in the mid-1960's, but he did not have a specific sighting or any recent reports. Today Swinhoe's Pheasants are probably no longer found south of the town of Heng Chun at Lat 22° N (Figure 1). They were still found just north of this area in the mountains south of the Feng Kang-Taitung cross-island highway.

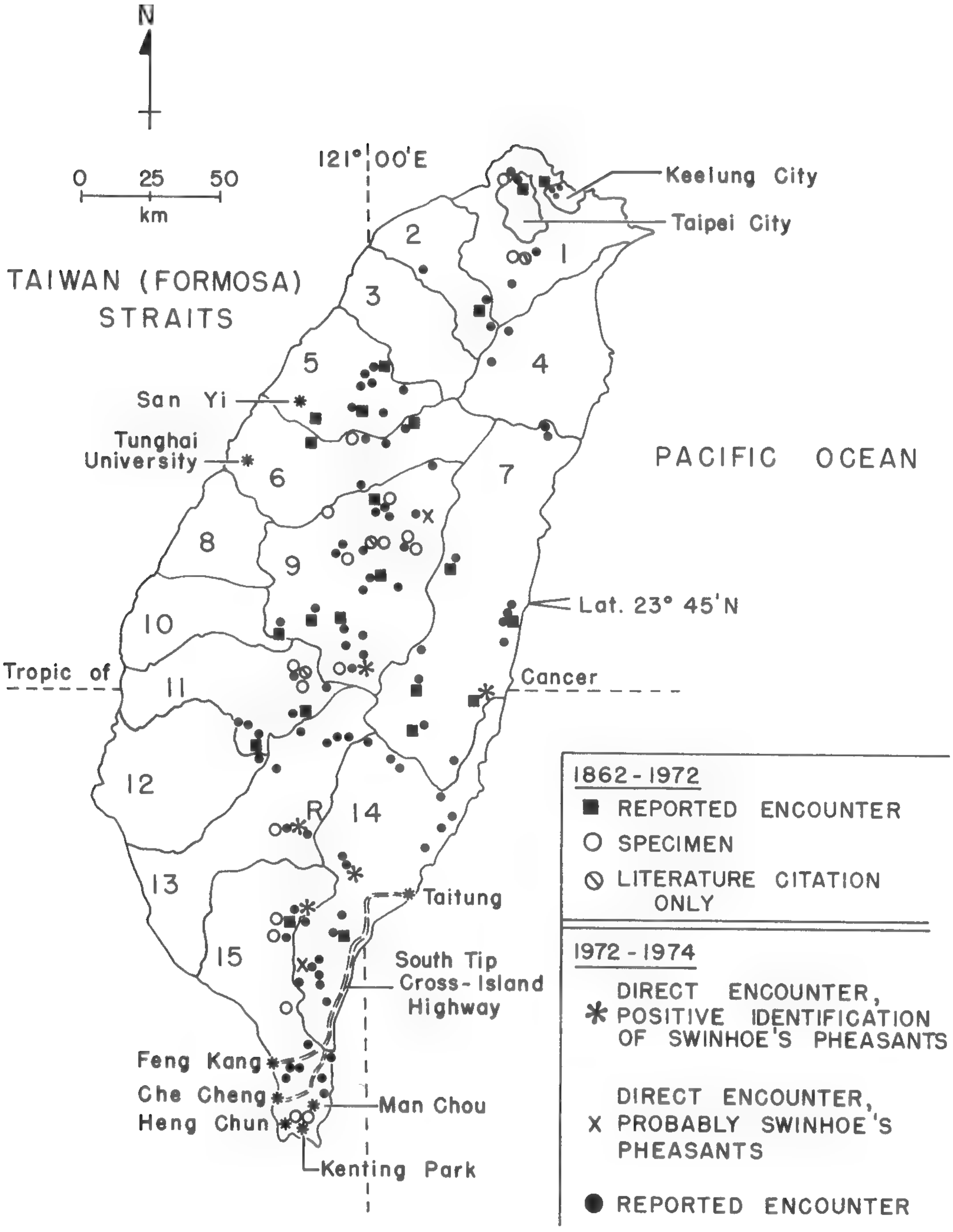
At the north end of the island, there were five reports from mountains within the city limits of Taipei and Keelung (Figure 1). We discovered Swinhoe's Pheasants in the geographically isolated Coastal Range (Figures 2 and 4). As far as I know, neither specimens nor sightings have ever been reported from these mountains. The Coastal Range is separated from the Central Mountains by populated and developed lowlands. In 1973 and 1974, Swinhoe's Pheasants were found from the southern end of the Coastal Range northward to about Lat 23° 45′ N (Figure 1). We received no reports north of this point, where the mountains are lower and more heavily disturbed by man. Swinhoe's Pheasants have probably disappeared now from similarly isolated low hills southeast of Sanyi (Miaoli): Mts. Kuantao and Chen Chung (Figure 3). The most recent sighting from these hills was late in 1971. Pheasants inhabiting Kuantao and Chen Chung mountains, the Coastal Range, the mountains north of Taipei, and the hills south of the Feng Kang-Taitung highway probably represent discrete populations reproductively isolated from each other and from populations in the central mountains by intervening valleys which are heavily cultivated and populated. Similarly, the Ta Chia and Lanyang river valleys (Figure 3) probably separate the pheasants living in the Hsueh Shan Range (Figure 2) from those in the Central Mountain Range. Other possibly discrete populations exist (Figure 3).

Elevation

Hachisuka and Udagawa [*8*] wrote that Swinhoe's Pheasants were usually found between 900 and 2,100 meters but could also be found "in any low place" where the forest was dense. Evidence from our field studies generally agreed with this. The lowest direct and reported encounters were at 300 and 100 meters respectively in forested mountains along the east coast. Another direct enounter was made at 800 meters in the Central Range, but most were made between 1,500 and 2,300 meters. One reported sighting came from close to 2,500 meters. Swinhoe's Pheasants can be expected to be found at higher elevations in southern parts of the island because the broad-leaved forests which they prefer grow at higher elevations there than in the north [*23*].

Habitat

Swinhoe's Pheasant was "a true jungle bird" according to Swinhoe [*18*]. Variations of this general description have endured: dense forest [*21*], thick and dense forest [*8*], jungle dense with rich subtropical vegetation [*26*]. Most of our direct sightings were made in primary, undisturbed evergreen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1862 - 1972
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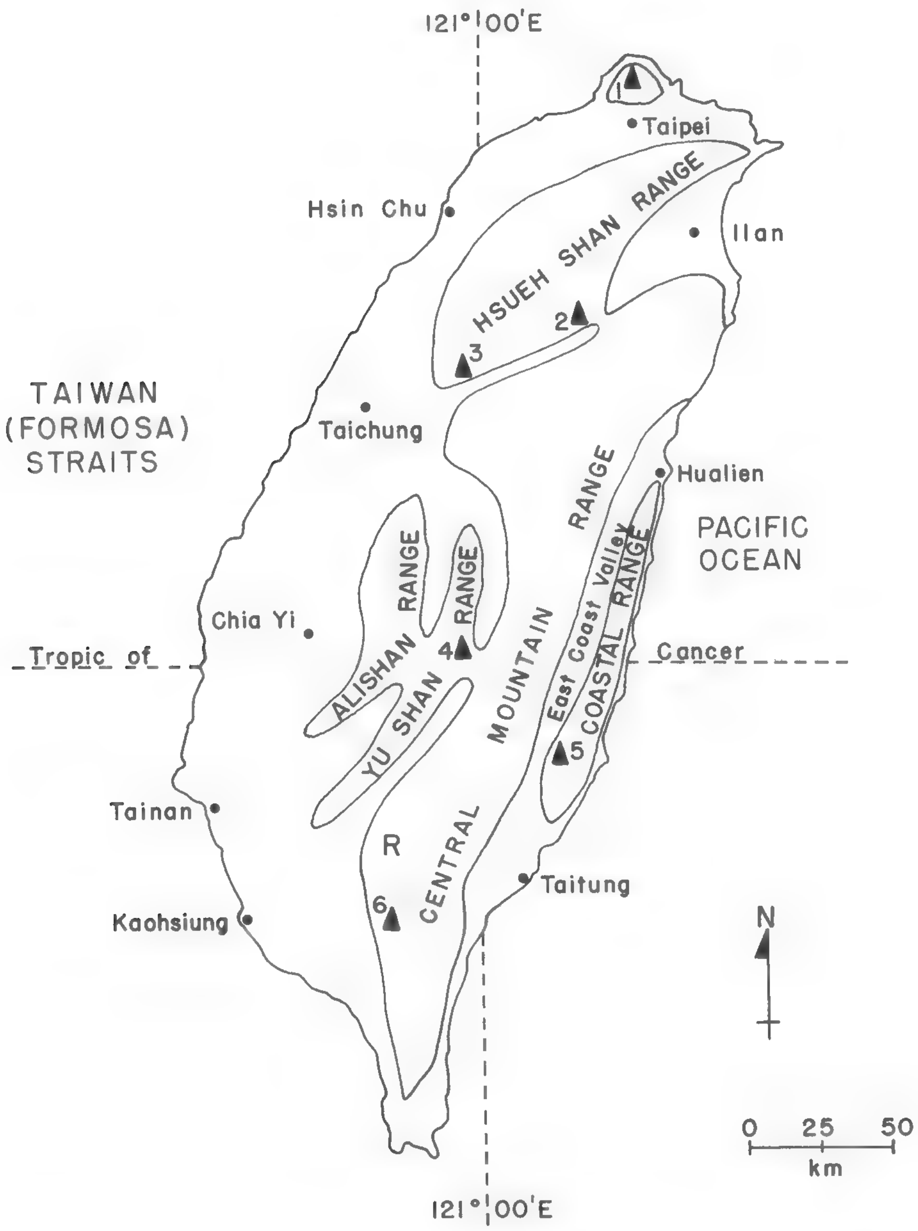
O SPECIMEN
⊘ LITERATURE CITATION ONLY
1972 - 1974
✱ DIRECT ENCOUNTER, POSITIVE IDENTIFICATION OF SWINHOE'S PHEASANTS
X DIRECT ENCOUNTER, PROBABLY SWINHOE'S PHEASANTS
● REPORTED ENCOUNTER

Figure 1. Map of Taiwan showing records of Swinhoe's Pheasants from 1862 and 1974. Data taken from the literature, museum specimens, and direct and reported sightings. Smaller asterisks indicate place names; larger asterisks indicate direct encounters. Counties are numbered as follows: Taipei (1), Taoyuan (2), Hsinchu (3), Ilan (4), Miaoli (5), Taichung (6), Hualien (7), Changhua (8), Nantou (9), Yunlun (10), Chiayi (11), Tainan (12), Kaohsiung (13), Taitung (14), Pingtung (15). The symbol **R** in Kaohsiung County (13) indicates the location of the Chu Yun Shan Forest Reserve mentioned in the text.

hardwood forests between 1,800 and 2,300 meters. These forests were strikingly different from the jungle image suggested by the earlier writers above. Forest interiors were shady and park-like. Sun filtered through the canopy, projecting dappled patterns of shifting dark and light on the gently inclined slopes. Shrubs and ferns were scattered and not obstructive. Liu [*12*] characterized this type of community as warm-temperature montane rain forest. Dominant species were oaks *(Castanopsis carlesii, Cyclobalanopsis longinux, Lithocarpus amygdalifolia)* and laurels *(Cinnamomum randiense, Actinodaphne nantoensis, Machilus zuihoensis)*.

Height of the closed canopy in the Reserve ranged from 10 to 15 meters, with some trees from 15 to 30 meters. Understory hardwoods ranged from 3 to 15 meters in height and were more closely spaced than the larger canopy trees. Woody lianas were present in some places. Ferns and shrubs were scattered. A heavy leaf and twig litter covered the ground along with numerous rotting trunks. Slopes usually ranged from 20 to 40 degrees but numerous flat or only slightly inclined areas up to 2,000 square meters in size existed.

In this type of habitat, vision across the forest floor at "bird's-eye level" ranged from 25 to 50 meters and even farther, depending on terrain. Pheasants cannot run for a thicket, as a Ring-necked Pheasant *(Phasianus colchicus)* might do in low elevation grasslands. They can only run away until out of sight. Information available from reported sightings and interviews tended to support the idea that Swinhoe's Pheasants prefer habitats with scarce ground cover.


121°00'E
1
Taipei
Hsin Chu
HSUEH SHAN RANGE
Ilan
2
3
TAIWAN (FORMOSA) STRAITS
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RANGE
Hualien
PACIFIC OCEAN
ALISHAN RANGE
YU SHAN RANGE
Chia Yi
4
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5
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Figure 2. Map of Taiwan showing mountain ranges and important peaks (after Wang, 1947). Important mountains noted (▲) include Chi Hsing (1), 1,120 m; Shao Lai (2), 2,307 m; Yu (3), 3,950 m; Kuan Tao (4), 889 m; Chen Chung (5), 559 m; Hohuan (6). The symbol **R** in the lower part of Taiwan indicates the location of the forest reserve mentioned in the text.

One direct encounter occurred at 800 meters in the Central Range in a habitat I judged to be mature secondary forest. Most of the canopy trees were 10 meters or less in height. Some taller and thicker stems (up to 100 cm dbh) appeared to be remnant individuals of the original forest. Beneath a partially open canopy grew a moderate undergrowth including shrubs, ferns, lianas, and rattan *(Calamus* sp.). A rocky substrate contained numerous exposed stones and heavy leaf litter. Slopes ranged from 40 to 50 degrees, but gentler areas from 10 to 20 degrees were present.

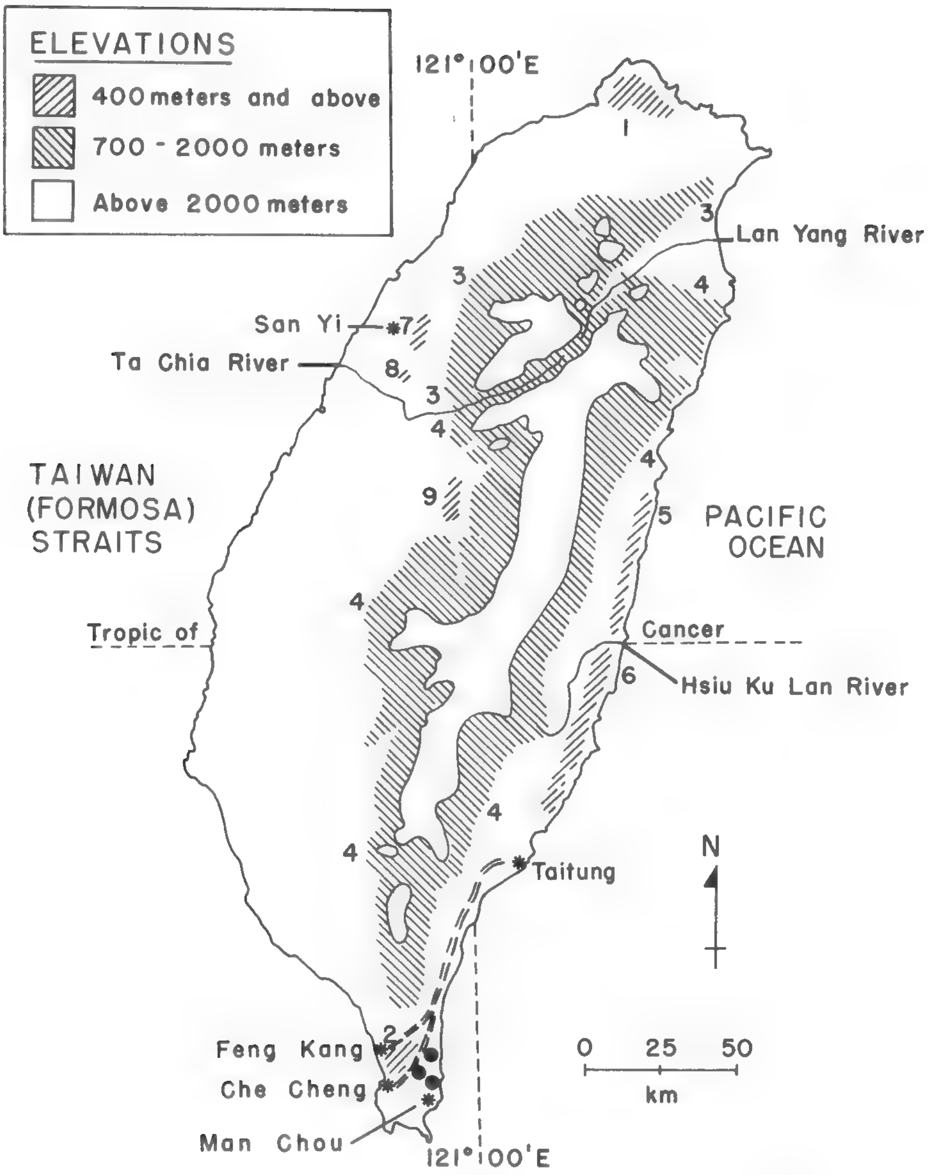
Another direct encounter occurred at 300 meters in the Coastal Range. Habitat there was mixed bamboo-hardwood forest . The dominant bamboo ranged from 5 to 10 meters in height. It grew in clumps of 20 to 30 stems, with clumps spaced 2 to 3 meters apart. The scattered hardwoods emerged slightly above the bamboo, and together they formed a closed canopy. Scarce ground cover included scattered ferns and wild taro (*Alocasia* sp.). Heavy leaf litter covered a stony substrate. Slopes were 50 to 60 degrees. This habitat resembled a secondary successional stage described by Liu [*12*]. He noted that in clearing a forest for shifting cultivation, the bamboo rhizomes escape destruction. When the area is abandoned, the bamboo grows back quickly to form a dense cover. Under natural conditions and after a "long period," the bamboo will begin to disappear due to a process of soil degradation. When this happens, the hardwoods begin to reappear.

Early reports indicated that Swinhoe's Pheasants were found in primary mixed forest and possibly in pure coniferous forests on rare occasions [*10, 14*]. Of the 106 sightings in primary habitat reported to us, about one-third (36) came from mixed forest. We saw none in primary mixed forest but were in an excellent position to test pheasant preferences for mixed forest. In the Reserve, we made all direct sightings in pure hardwood forest. These sightings occurred up to the elevation where conifers began to appear. We recorded no pheasants in the adjacent mixed forests of the Reserve (Figure 5).

In northern Taiwan, Mt. Shaolai (Figure 2) had pure hardwood forests on its southern slopes grading into conifer forests on its northern slopes at the same elevation (2,000 m). An experienced trapper in this region said that he caught Swinhoe's Pheasants almost exclusively in the pure hardwood forests on the southern slopes. Again, in a limited area, Swinhoe's Pheasants preferred pure hardwoods to mixed or pure coniferous forests. Mt. Shaolai is part of the Hsueh Range mentioned above where Kano did his work and reported Swinhoe's from mixed forests.

Out of 129 reported sightings, 106 (82%) occurred in primary habitat and 23 (18%) in secondary habitat (Chi Square, $P<0.005$). A similar preference was reflected in the interviews. Out of 80 respondents, 59 (74%) said that Swinhoe's Pheasants could be found in primary habitat types and 21 (26%) said they could be found in secondary habitats. These results are also significant (Chi Square, $P<0.005$). These 209 respondents spent more time in all seasons in secondary habitat types than in primary types, yet they reported significantly more sightings in primary types than secondary. This would preclude the possibility of bias resulting from unequal coverage of the different habitat types.

Several reported sightings from secondary habitat types indicated that primary or mature secondary hardwood forests were nearby: One pheasant was sighted moving from a cassava field into virgin forest; another on the edge of primary and replanted forest; a third in natural secondary forest


ELEVATIONS
400 meters and above
700 - 2000 meters
Above 2000 meters
121° 00'E
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Ta Chia River
Lan Yang River
TAIWAN (FORMOSA) STRAITS
PACIFIC OCEAN
Tropic of Cancer
Hsiu Ku Lan River
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Figure 3. Map of Taiwan showing the approximate distribution and possibly disjunct populations of Swinhoe's Pheasants. The locations of the postulated pheasant populations are Mt. Chi Hsing (1); southern (2); north central (3); south central (4); north coastal (5); south coastal (6); Mt. Kuan Tao, 889 m (7); Mt. Chen Chung, 559 m (8); Chi Chi, 1,396 m (9). Other populations are indicated by solid circles at the south end of the island.

surrounded by cultivation and second growth; and a fourth in a bamboo plantation with virgin hardwoods on the slopes above it.

Other people who said that Swinhoe's Pheasants could be found in secondary habitats qualified their statements by noting that such habitats showed characteristics of primary forests, including maturity of trees, replanted forests with little undergrowth, a closed canopy, or lack of grassy areas.

Reported sightings like these indicated that Swinhoe's Pheasants may be dependent on primary forest but venture out at times into surrounding second growth. We observed this behavior pattern when pheasants came out of the virgin forest in the Reserve to feed in the second growth along the road.

On the basis of these direct and reported sightings, it is apparent that Swinhoe's Pheasants prefer primary habitats (of all kinds) to secondary ones, but use second growth habitats to some extent. The data do not indicate whether or not Swinhoe's Pheasants are able to adapt entirely to life in secondary habitat types. The extent to which they can do this is one of the most important aspects of pheasant biology still to be determined.

Slope probably influenced pheasant distribution indirectly to the extent that it influenced vegetation types favored by the pheasants. Liu [*12*] noted that hardwood forests tended to be found on the fertile and mesic sites of gentle slopes. Of 47 records of slope angle for Swinhoe's Pheasants, 41 (87%) were on slopes of 40 degrees or less, 31 (66%) on slopes of 30 degrees or less, and 18 (38%) on slopes of 20 degrees or less. Our sightings plus those of the people interviewed indicated that Swinhoe's Pheasants preferred gentle slopes. A small number of those interviewed (8) said that pheasants usually were found on flat terrain or gentle slopes. To the extent that Swinhoe's Pheasants inhabit mixed or coniferous forests they will probably be found on steeper slopes.

Behavior

Escape

Swinhoe's Pheasants were vocally silent most of the time. We never heard the "crowing defiant note" mentioned by Swinhoe [*18*], nor any call reminiscent of the crow of the Ring-necked Pheasant. With 50 direct encounters and 341 party hours in the Reserve, we heard vocalizations on only ten occasions. Of these, only three were thought to have been given independently of human intrusion. We collected these data from mid-December to early April, a period which included the courtship and early breeding seasons when one might have expected to hear more vocalizations.

When undisturbed, wild Swinhoe's Pheasants were virtually noiseless in walking across the forest floor. When the leaf litter was damp or the ambient noise level high they were usually impossible to hear.

When escaping on foot, Swinhoe's Pheasants made only slightly more noise than when undisturbed. Escape was indicated by the snapping of twigs and the rustling of leaf litter. The noise seldom lasted more than a few seconds, then the forest fell silent again. This pattern suggested that pheasants moved only a short distance before slowing to a silent walk, or possibly stopping altogether. In most cases, they could not be followed or located again by sound or sight once they had "escaped."

In general, people walking through the mountain forests of Taiwan make sufficient noise to give ample warning of their approach, and pheasants are probably able to avoid most contacts by slipping easily and quietly away on foot. When moving up- or down-slope, Swinhoe's Pheasants almost invariably took a diagonal track. At one particularly steep site (40° to 50°), a male took a switch-back path, angling back and forth down the slope as it escaped.

Pheasants usually maintained a rather erect posture when fleeing, but in one instance a pheasant adopted a skulking "rodent run" posture as it hurried away. The slope at this site was less than 10 degrees. Occasionally a pheasant "froze" for several seconds before leaving.

Flushing was not a characteristic means of escape for Swinhoe's Pheasants. In 58 direct encounters, only two flushed. An adult female flew to about 3 meters off the ground from a road construction slash and then flew to the nearest trees. It did not vocalize.

As this female flushed, its tail feathers were spread, conspicuously displaying the chestnut outer feathers contrasting with the brown, barred central ones. Davison [*4*] concluded on the basis of observations of captive pheasants that this type of tail pattern, in this and several other species, serves as a "general alerting signal to conspecifics." He indicated that the signal might be used in flight or on the ground as a means of calling the brood. The whirring of the wings was the first sign of flushing and was more noticeable to us than the visual signal of the spread tail pattern.

The other bird we flushed was an adult male. It took off from the forest interior above the Reserve logging road. It emerged 6 to 8 meters over the road and flew out horizontally away from the mountain slope. By the time it reached the first trees below the road it was perhaps 15 meters above the mountain slope. It flew into the forest canopy and disappeared. The observed part of the flight lasted about ten seconds. It called rapidly and sharply when it flew. Judging by the vocalization, the pheasant continued to fly down the slope, possibly stopping once or twice en route. The flight pattern was flap-and-glide.

Adaptive Coloration

The brown plumage of female Swinhoe's Pheasants is speckled with yellowish triangular and arrow-shaped markings. This effectively cryptic pattern was difficult to detect against the background of the sun-dappled forest floor and may explain, in part at least, why we saw females on only six occasions while recording males 48 times.

The plumage of the adult male Swinhoe's Pheasant is flashy (see color plate). When a male moved quickly to escape, the movement of white back and rectrices across the darker background of the forest floor was often conspicuous. When the bird walked slowly or stood still, it was more difficult to see than one might expect. The color pattern became disruptive. In discussing adaptive coloration, Cott [*2*] pointed out that white marks on a dark body was the most effective optical pattern for breaking up body contours and masking half-tone shading of animals living in heavily-shaded forests.

The full-grown male in its first year lacks white and is generally dull dark blue. Its plumage would make it easy to miss in the dark interior of a heavily-shaded broadleaf forest. We did not see a single male in this plumage in the wild.

Adaptability to Ground Conditions

In areas of second growth where ground cover was dense and tangled, Swinhoe's Pheasants moved awkwardly, stumbling and tripping from time to time. In contrast, their movement across the floor of the forest interior was graceful and silent. The scarce ground cover provided little obstacle to easy passage. Their long legs enabled them to step easily over branches and twigs and to cause almost no disturbance to the leaf litter. The Formosan Hill Partridge *(Arborophila crudigularis)*, a galliform sympatric with Swinhoe's Pheasant, tended to make more noise in walking through the forest. Closer to the ground because of shorter legs, it shuffled and disturbed the leaf litter as it walked. We learned to distinguish these two species with considerable accuracy on the basis of the noise each made when walking.

Figure 4. Northern part of the Coastal Mountain Range as seen when looking east across the valley from the Central Mountain Range west of Hualien.

Daily Activity Levels

Wild Swinhoe's Pheasants were most active in the early morning and late afternoon. In the Reserve, most sightings (82%) were made before 08:00 hours (26) and after 16:00 in the afternoon (19) in three periods between mid-December and early April. Ten sightings (18%) came between 08:00 and 16:00. We spent more party hours surveying during midday (185 hours from 08:00 to 16:00) than during early morning and late afternoon hours combined (164 hours: 06:00 to 08:00, 16:00 to 19:00). Yet the number of pheasant encounters per party hour was 5.4 times greater in the early morning or late afternoon than during midday, a significant difference (Chi Square, $P<0.005$).

We made earlier sightings (06:25/06:20/06:05) in each of the three periods as the days grew longer from December to early April. The latest sightings also tended to get later as the days grew longer, from 17:30 in December and February to 18:05 at the end of March. In the late afternoon, there were an increasing number of sightings from 17:00 to 18:00 and a decreasing number from 15:00 to 17:00 as winter turned to spring.

From 08:00 to 16:00, we saw only one pheasant in the open in full direct sun. It crossed the road quickly and entered the forest. Two other birds sighted outside the forest or at forest edge were in heavy fog. Our other encounters (6) during midday hours occurred inside the forest. These sightings indicated that Swinhoe's Pheasants kept to heavily shaded forests during the day, except on sunless days when they occasionally ventured into the open.

The level of activity and movement from 08:00 to 16:00 appeared to drop, even inside the forest. Ninety-two hours of observation from two blinds deep in the forest at all hours of the day produced only three sightings, two before 08:00 and one after 16:00. Taka-Tsukasa [*21*] reported that this species in captivity "takes a short walk in the morning and evening, to get food and drink. The rest of the day, it spends its time by sitting still on a high perch." We saw no wild pheasants roosting nor heard them flying to a roost during the day, but it was apparent that they remained relatively inactive during these hours.

Roosting

Evidence from this study indicated that Swinhoe's Pheasants roost in trees at night. Among those people we interviewed with an opinion, 27 said that Swinhoe's Pheasants roosted in trees and 6 said that they sometimes roosted in groups in trees, at least at certain times of the year. One reported sighting came from a hunter who had shot three adult males and five females roosting in one tree in December. Each pheasant was on a different branch of the tree. Roosting pheasants are discovered by chance at night when hunters with lights search for nocturnal flying squirrels. Another hunter in October shot a single adult male roosting on a lower branch away from the trunk.

Direct evidence of roosting pheasants was scanty but worth describing. I heard one bird come down from its roost at 06:25, fifteen minutes after the first light of dawn and one hour ten minutes before sunlight first hit the forest floor. For the next hour and forty minutes, the bird remained 10 to 15 meters up-slope from me and out of sight. Intermittent leaf rustling indicated the bird was moving around and probably feeding. At 08:05, the pheasant apparently saw me move slightly and began to vocalize. It called for several minutes and then moved up-slope and stopped calling. I did not see or hear it thereafter.

Later that morning, I inspected the area in which the pheasant had probably roosted. An opening in the forest canopy had produced a dense undergrowth of saplings 6 to 8 meters tall (<1 centimeter dbh) and small understory trees (2.5 to 3.5 centimeters dbh). Saplings were spaced a meter or less apart. As judged by the sound of the bird dropping to the forest floor the roost was probably 1 to 2 meters off the ground.

On another occasion, I heard a pheasant fly from the forest floor to a tree late in the afternoon (18:05). The sun had set and it was getting dark. Several hours after dark, we searched the area with head-lamps hoping to locate the roosting pheasant but without success. The suspected roost site was 25 to 30 meters down-slope from the road in virgin hardwood forest. Canopy trees were 10 to 15 meters tall, 30 to 100 centimeters in dbh. Understory trees were 3 to 10 meters in height, less than 30 centimeters in dbh, and more closely spaced than the canopy trees. Slope was 30 to 40 degrees.

In both these cases, the birds apparently were alone. No other birds were heard. The first encounter was in mid-February and the second was in late March. Perhaps by these times, the females had begun tending nests. Under these conditions, one might expect males to roost singly. I have no direct evidence of gregarious roosting.

Feeding

Much of the feeding activity that we observed took place in the early morning and late afternoon, corresponding to the periods of most frequent sightings. Pheasants often fed in herbaceous ground cover at the road's edge in the Reserve and in man-induced second growth above and below the road. Similar conditions of second growth were created naturally when large canopy trees fell to the ground, as in the roosting area described earlier.

The Swinhoe's Pheasants we saw seldom used their feet to open areas on the forest floor. They usually fed by digging with their bill. When the feet were used, the pheasant stood on one leg and deftly used the toes of the other foot to pick apart the leaf cover only enough to reach the food. This produced little noise and contributed to the overall silence of the bird as it moved through the forest.

The foraging behavior of parties of Formosan Hill Partridges was notably different. They gave the ground litter two or three swift kicks to the rear with alternating feet. The litter flew out behind. As they did this, they backed up and lowered their head to feed in the area just cleared. As a result, partridges made considerably more noise in foraging than Swinhoe's Pheasant. Partridges also tended to tear up the forest floor, scattering the leaves and leaving conspicuous openings down to the partially decomposed organic matter. On two occasions from a blind, we saw Swinhoe's Pheasants feed across an area which had numerous signs of partridge feeding. The

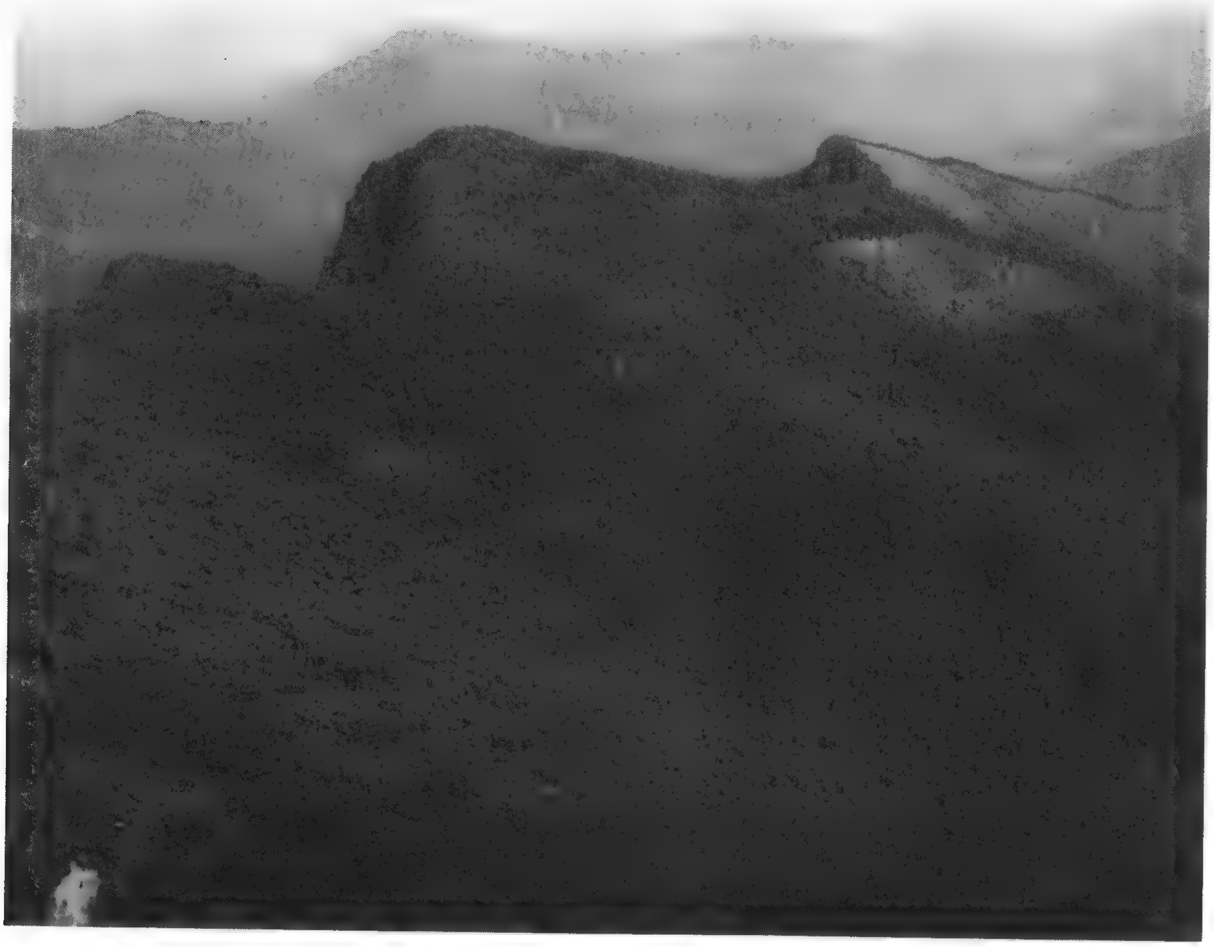


Figure 5. Looking south along a ridgeline in the Chu Yun Shan Reserve. Eastern slopes are generally less than 40 degrees. Darker trees (lower right) are conifers mixed with hardwoods at higher elevations. Clear cut forest can be seen to upper right and logging road in center.

pheasants seemed to be feeding frequently in the openings cleared earlier by the partridges. In these instances, digging and probing with the bill was the only means of feeding used by Swinhoe's Pheasants.

This relationship between pheasant and partridge was reported independently by five of the people interviewed. They said that Swinhoe's Pheasants often followed directly behind the partridges, and one even went so far as to say that the pheasants "robbed" the partridges of food. Neither of these activities was observed by team members, but it does seem possible that a commensal relationship exists. The Formosan Hill Partridge is sympatric with Swinhoe's Pheasant over much of the latter's range [*16*].

When desired food items were just out of reach, we saw pheasants easily jump, using the legs only, to get the morsels. On one occasion, we were close enough to a feeding adult to hear a call that accompanied the feeding. The field notes described it as "soft, liquid murmurings and musings." It was barely audible from 15 meters in an environment with little ambient noise.

Vocalizations

We heard three types of vocalizations during the course of this research. For discussion purposes they are called the murmuring, plaintive, and sharp calls.

Murmuring call—This type was described above and accompanied feeding behavior of a single adult male.

Sharp call—A high, sharp, rapid *deek-deek-deek-deek* with a slightly metallic ring. In 53 encounters with males, the only male that flushed gave this call. It was almost certainly a high intensity alarm call. The one female we flushed did not vocalize at all.

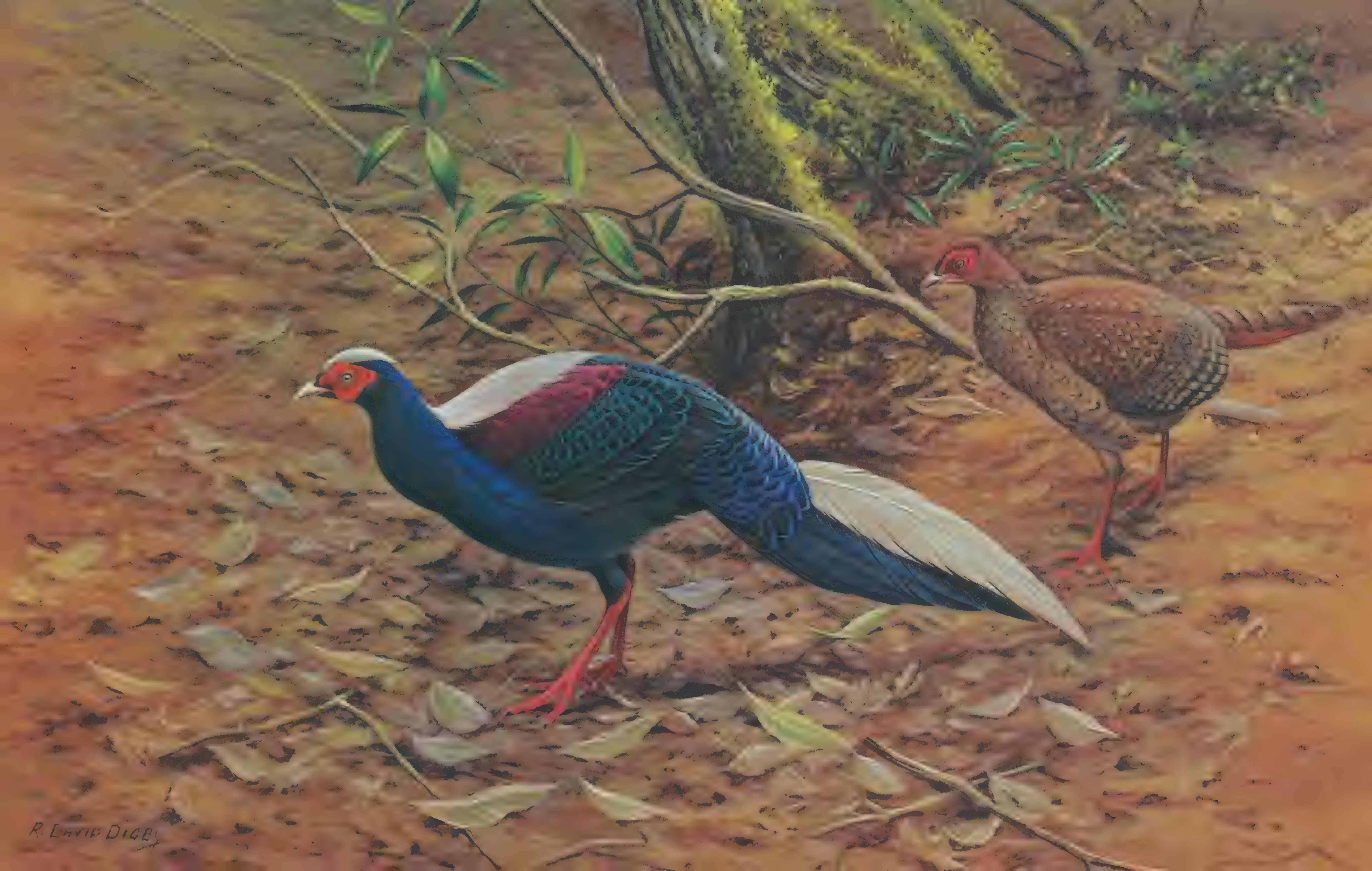
Plaintive call — This vocalization we heard eight times. It was a loud, penetrating, rather high and plaintive call given at different rates and with some variation. At times the syllables were repeated persistently and in rapid succession (*oot-oot-oot-oot*, etc.), broken with a pause only at long intervals. At other times, the syllables were uttered more slowly as separate units with discernible pauses between them. The call easily carried 100 meters. Only males were definitely identified giving this call.

On three ocasions, sharp, metallic clicking or chirping noises punctuated the end of each *oot* syllable. This combination of sounds seemed to be produced by the same bird, but it sounded like such an improbable combination as to be coming from two birds. The most complex variation of the plaintive call added a sliding inflection downward, then upward, in pitch between occasional *oot* syllables.

The plaintive call seemed to signal mild alarm in response to the cautious approach of human observers. The rate of calling appeared directly related to the intensity of the bird's response to the intrusion.

On one occasion, we heard the plaintive call in a context probably related to the presence of another pheasant. An adult male, deep in the forest, began giving the plaintive call punctuated with sharp clicking. Shortly, a second bird, unseen, began calling about 30 meters away. As nearly as can be judged by the location of the calls, the two birds drew closer together inside the forest. They appeared to meet, or at least come close together, at which time the vocalizations stopped. If both were males and were calling independently of the human presence, as seems likely, then the plaintive call may have been related to territorial advertisement.

Swinhoe's Pheasant, *Lophura swinhoii*. Painting by Ronald David Digby.


R. DAVID DIGBY

Seasonal Conspicuousness

Conspicuousness, as used here, reflects a tendency of pheasants to come out of the forest, either along thoroughfares or close to the forest edge.

Significantly more sightings, direct and reported, were made during the dry season than the rainy season (Chi Square, $P<0.005$).

In the Reserve, the index of conspicuousness for direct sightings (i.e., the number of encounters per party kilometer) showed a seasonal decline from December 1973 (0.41) to February (0.15) and early April 1974 (0.04). It declined again from December 1974 (0.04) through March 1975 (0.00). Party hours and party kilometers increased from December to March and April during both winter seasons as the index of conspicuousness decreased; thus, the decreasing index was not correlated with decreasing survey effort and does not reflect a research bias. Index values for December 1974 (0.04) and March 1975 (0.00) were lower than the values for those same months in 1973 and 1974 (0.41 and 0.04, respectively). But the index trend was the same both winters during which rainfall was increasing. Interviews also supported the tendency toward greater conspicuousness during the dry season (7 vs. 3).

There appears to be, therefore, a strongly positive correlation between conspicuousness and the seasonality of precipitation. Other evidence supports this. On a daily basis, 96 percent of the direct sightings (56 of 58) were made on days which had had no rain prior to the time of observation. Whenever possible, the field team conducted surveys during and after rainy periods, as well as in good weather, so that these results were not biased by research methodology. If future investigations prove this relationship to be true, the question then arises as to what drives Swinhoe's Pheasants deeper into the forest away from roads and trails during the rainy season. The answer may be rain. The forest interior is often drier during rain because of the thick, closed canopy of broadleaved trees, which reduces the quantity and impact of precipitation reaching the forest floor.

Courtship

The lateral courtship display has been described in captive Swinhoe's Pheasants by Taka-Tsukasa [*21*], Delacour [*5*] and Wayre [*26*]. Stokes and Williams [*17*] described courtship feeding. We did not see courtship or cleared display areas of wild Swinhoe's Pheasants nor was either one reported to us.

Mating System

Referring to the mating system of the genus *Lophura* as a whole, Delacour [*5*] said "Opinions differ as to whether they are monogamous or polygamous in the wild state. It may vary with the species, but most pheasants at liberty are polygamous and do not really pair up."

Wayre (pers. commun.) thinks that Swinhoe's Pheasants may be monogamous in the wild based on his experience with feral birds introduced on Brownsea Island off the coast of England. In the Pheasant Trust Annual Report (1968), these Brownsea Island pheasants were described as breeding and rearing young in pairs. One pair was described as having "its territory" in dense rhododendron cover.

I have no conclusive evidence from field research as to the mating system of wild Swinhoe's Pheasants. With 58 direct encounters of wild Swinhoe's

Pheasants in five months (December, February to May), a male and female were seen together on only one occasion (mid-February). All other direct sightings were of single males. Among reported sightings, 85 percent (70 of 82) were of single males or single females and only 15 percent (12 of 82) were seen as pairs. There were no reported sightings of a male with a harem, although eight people, when asked, said that this situation occurred.

I suspect that further research will show that Swinhoe's Pheasants tend to be polygamous in the wild and that males spend very little time in the company of females during courtship and nesting periods. This seems consistent with the data we have obtained so far and with the behavior of a species in which solitary cocks with elaborate plumage maintain small territories.

Gregariousness

We saw no groups of wild Swinhoe's Pheasants. Reported sightings and interviews indicated strongly, however, that Swinhoe's Pheasants are gregarious, at least at certain times of the year. Groups composed of male, female, and young reportedly were seen in October and December. Groups of males and females were shot roosting together in December and January. Wayre [*24*] reported flushing seven Swinhoe's Pheasants in May 1967 and thought they may have been a family group because they were found in a small area.

Among 18 sightings that we recorded in mid-December, just before the beginning of the breeding season in the Reserve, we saw no groups and have circumstantial evidence of only solitary roosting. It would seem that gregariousness during the non-breeding season does occur, but that it may not necessarily be regular or obligatory.

Territoriality

We collected data relating to territoriality in the Reserve in a tract of primary hardwood forest through which a narrow and lightly used logging road passed. Sightings were made along a 4.2-kilometer stretch of this road which we had marked in 100-meter intervals. Although individual pheasants were not marked, the survey techniques used provided information from which one might reasonably infer territoriality. This was based on four lines of evidence: (1) repeated observations of a male at the same spot, (2) simultaneous sightings of two males close to each other, (3) sequential sightings of male pheasants in time and space, and (4) movement of males with respect to a hypothetical territorial boundary.

Pheasant encounters were scattered at varying intervals along the logging road. Encounters tended to be clumped in certain areas in certain months: Km 3.0 to 4.4 (11 encounters) and Km 5.5 to 6.6 (7 encounters) in December; Km 2.5 to 2.7 (10 encounters) in February; Km 2.45 to 2.7 (7 encounters) in March. In areas where encounters were clumped, some regularity in spacing was discernible. In December, for example, we saw cock pheasants at Km 3.0, 3.1, 3.2 and 3.3, all equidistant intervals of 100 meters. In February, we recorded nine encounters at Km 2.5, 2.6, and 2.7. In March and April, we made two sightings at Km 2.45 and three at Km 2.55. Other encounters also came at 100-meter intervals: Kms 4.3/4.4, 5.5/5.6, 6.0/6.1.

One would expect territories to manifest themselves most clearly in areas where pheasants were concentrated and competing for available resources, including space. One interpretation of these observations assumes that the repeated sightings of cocks at one site represented one individual and that sightings made at 100-meter intervals represented different, neighboring males. There was some evidence to support this. Males recorded at points one-tenth of a kilometer apart within 10 to 25 minutes on three occasions suggest the presence of different males on their territories.

There is some evidence that the road itself may have acted as a territorial boundary, since two cocks were observed at almost the same time above and below the road, and four sightings of a male at Km 2.7 were of a bird at the same point down-slope. Three of these were within two days in February, one of them was a month later in March. We sighted no pheasants above the road at Km 2.7.

If male Swinhoe's Pheasants were territorial, as the observations suggested, then one would expect them to have some means of establishing and maintaining the territories. In over 340 party hours in the Reserve, we heard pheasants call only once (Km 3.2) in a context that may have been related to territorial confrontation. If it was , it was the only one we witnessed. Vocalizations apparently played little or no role in territorial advertising by males in the Reserve. One person interviewed said that he had seen male Swinhoe's Pheasants "fighting" on several occasions and thought they might have territories.

Spatial and Temporal Changes in Distribution

A shift apeared to take place in part of the pheasant population along the Reserve road from December to the following February. In 18.25 party hours in December, seven encounters of males occurred from Km 3.2 to 4.4. In February, with 40.5 party hours, no sightings at all were made in that stretch. Instead, pheasants began showing up at that time in an area where we had made no sightings the previous December (Km 2.5 to 2.7).

From mid-February to the end of March, there appeared to be another shift. In February, we sighted males four times in 40.5 party hours at Km 2.6, above and below the road, but saw none at that point in March with almost 160 party hours. In March, however, pheasants were sighted at three points below the road (Km 2.45, 2.5, 2.55) where none had been sighted in February.

The shift might have been related in some way to the change from non-breeding to breeding status. However, the shift of one kilometer or less provided no discernible or substantial differences in habitat, elevation, slope, and aspect. Another explanation may be that some of the December sightings were of individuals displaced by logging from their former range between Km 6.6 and 6.8. These individuals may have been in the process of relocating themselves following the destruction of their forest (Figure 5).

It should be emphasized that these inferences related to territoriality and population shifts are based on circumstantial evidence related to observations of unmarked birds. They cannot be proved but are presented as reasonable possibilities based on the evidence at hand.

Population

Size of Population

In 1966, the "Red Data Book" [9] listed Swinhoe's Pheasant as "extremely rare in the wild." A close reading of the "Red Data Book" suggested that possibly only a few hundred existed. Viewed against this estimate, the current data suggest Swinhoe's Pheasants may have been considerably more numerous in 1974 than conservationists thought.

Among those people interviewed who had an opinion, 53 percent (62) thought they were common. There were direct and reported sightings of 331 Swinhoe's Pheasants, and we tallied 501 birds that were known to have been taken from the wild, a total of 832 birds in two years. This means that an average of about 400 birds were sighted or taken each year. Since our field surveys and interview coverage were by no means complete for the whole island, the figure doubtless fell considerably short of the total number of pheasants actually seen and taken each year. And that figure probably represented only a small fraction of the total wild population. Given the secretive nature of the pheasants and the rugged terrain in which they live, it was difficult even to approximate what their numbers might have been. I suspect, however, that in 1974 Swinhoe's Pheasants almost certainly numbered in the thousands, perhaps 5,000 to 10,000, rather than in the hundreds as implied in the 1966 "Red Data Book."

Trend of Population Change

Several lines of evidence leave little doubt that the population of Swinhoe's Pheasants has declined over the years. The range of pheasants has been decreasing over the years (as discussed earlier) and with it their numbers have almost certainly declined. Among those we interviewed who had an opinion, 73 percent (90) said Swinhoe's Pheasants were less common today than they used to be.

None of those interviewed reported a crash in pheasant numbers or in take in recent years, so that the population decline has probably been a gradual one.

Sex Ratio

Of 287 pheasants seen in the wild (direct and reported sightings), 207 (72%) were males, 80 (28%) were females. The preponderance of males sighted was probably due to the fact that they were easier to see and more active, at least at certain times of the year, than females. Among birds known to have been trapped or shot, the sex ratio was more nearly even, 137 males (57%) to 105 females (43%). This difference in captured birds is statistically significant (Chi Square, $P<0.005$) but does not necessarily indicate an actual imbalance in sex ratio among living birds. Greater activity of males could make them more susceptible to being snared than females. Or perhaps the people interviewed tended to remember catching the colorful males more readily than females. On the basis of these considerations, the apparent skew in sex ratio could reflect a bias and Swinhoe's Pheasants may approximate a 1:1 sex ratio in the wild.

Breeding

Breeding Season

The known hatching date of four wild-collected eggs was 9 April 1973. Laying could have commenced as early as 3 March or as late as 7 March, based on an incubation period of 25 days [5] and a rate of laying of one egg every two or three days [*20*]. Egg-laying by wild birds in March agreed with Delacour's [*5*] observations of captive birds in which the Swinhoe's hen was "an early layer, usually starting in March."

Of those we interviewed who reported seeing eggs of wild Swinhoe's Pheasants, 12 (63%) reported seeing them in March, April, or May. Two females bearing developing eggs were caught by loggers in April 1973. The earliest egg reported was in February. Other egg reports were scattered from June through September (4) and in November (1). Based on these reports, the peak laying period appeared to be from March through May.

The earliest and only confirmed hatching date of chicks from wild-collected eggs was 9 April. Chicks were reported once each from the months of March, May, September, and October. Two people reported that Swinhoe's Pheasants breed twice a year: once in the early spring (March and April) and once in late summer or fall (August to November). These reports plus egg and chick reports from September to December may represent individuals that failed to nest for some reason during the spring and summer. There is no substantial evidence for two pronounced breeding periods during the year.

Clutch Size

Taka-Tsukasa [*22*] gave the clutch size in Swinhoe's Pheasants as five to eight eggs. Later workers indicated a larger clutch size: 6 to 12 eggs [*5*] and 6 to 10 eggs [*25*]. These figures presumably were birds that laid in captivity.

By extrapolation, a clutch of four eggs, taken from the wild on 25 March and hatched in captivity on 9 April, was incubated by the female for 10 days prior to being removed and was, therefore, complete.

People interviewed said that clutch size in the wild ranged from two to twelve. Most clutches (82%) were reported to range from three to eight. The latter more nearly approximates the range reported from early generations of captive birds (5 to 8) than the range reported from later generations (6 to 12). This suggests that clutch size in wild pheasants may be smaller on the average than clutch size in captive birds.

Nest Site

The Japanese collector Yonetaro Kikuchi reported that the nest of Swinhoe's Pheasant is "placed near the foot of a tree or under shelving rocks in the densest forest" [*21*]. He reported that the nest "is made of a few fallen leaves." Thirteen people interviewed on this project said that nests were lined with leaves (2), grass (7), or both (4). Three said the nest was only a bare depression in the ground. The team did not discover an active nest of wild Swinhoe's Pheasants but did receive a confirmed report of one. A farm family caught a female incubating four eggs on her nest in the Coastal Range at an elevation of approximately 500 meters. The nest was between the roots of a large tree and was protected from the rain. It was not lined, and the eggs were laid on bare earth. The surrounding habitat was primary or mature secondary hardwood forest on gentle slopes. The forest floor had heavy leaf litter and some rattan, according to the farmers.

Of those interviewed who had information on nest sites, 34 (74%) said Swinhoe's Pheasants nested on the ground and 12 (26%) said they nested in elevated positions. The ground sites most frequently mentioned (by 16 people) were next to a fallen tree or in open spaces underneath the trunk.

Nests were also reported among roots or in root cavities (3), among rocks (2), and amid clumps of vegetation (2). All these sites would provide some concealment and protection to the nest and hen.

Reports of nests in elevated positions were of interest since, except for the genus *Tragopan*, pheasants have always been considered ground nesters. Four people reported pheasants nesting on the top of rocks, logs, or stumps. Sites like these are usually within a meter or so of the ground and often have clumps of epiphytic vegetation growing on them which would provide concealment for the nest. Slightly elevated positions would also provide better protection from heavy rains and ground predators.

There were more reports of pheasants nesting in trees than nesting on the slightly elevated positions just discussed (8 vs. 4). I saw one of these tree nest sites. As far as I know, this is the only account of a tree-nesting member of the genus *Lophura*. The nest was discovered by a hunter in mid-September 1971. He shot the incubating hen when she flushed and found five eggs in the depression of a stub where the trunk had broken off. The eggs were "chicken-like" and had a "reddish tinge" to them. The nest was five meters off the ground. It was oval in shape. Nest dimensions two-and-one-half years later (1974) were as follows: depth, 12.7 cm; inner diameter (length), 22.9 cm; outer diameter (length), 38.1 cm; inner diameter (width), 17.8 cm; outer diameter (width), 33.0 cm. The nest was located between 1,600 and 1,700 meters elevation in northeast Pingtung County (Figure 1) on a north-facing slope in primary hardwood forest. The nest site was open to the north but was covered by light canopy vegetation and vines on the other sides and on the top. The nest depression was lined with leaves, but this was doubtless an accumulation of leaf drop in the two-and-one-half years since the nest was reportedly active. Vines grew around the rim of the nest stub and did not grow over the nest.

The identification of the nest as belonging to a Swinhoe's Pheasant came second-hand, yet several points make the report highly credible. An experienced hunter shot the bird, providing a reliable in-hand identification of the hen pheasant. The chicken-like eggs of reddish color could belong to no other species in that forest. With this particular report and the other more generalized reports of tree nesting, there appears to be strong evidence that Swinhoe's Pheasants do nest in trees some of the time.

Taka-Tsukasa and Kano [*22*] reported that Swinhoe's Pheasants bred between 1,200 and 1,800 meters in elevation on the Hsueh Shan Range (Figure 2), but expanded their altitudinal range from 600 to 2,100 meters during the non-breeding season. The collector Kikuchi [*21*] also reported a narrow range in breeding elevation: 4,000 to 5,000 feet. No reports of a restricted altitudinal breeding range were received during the project. The confirmed nest report in the Coastal Range was at an elevation of approximately 500 meters.

Predators

Nothing has been published in the literature about predation on Swinhoe's Pheasants. The only evidence of predation seen during this project was that by man. Perhaps the most likely mammalian predator is the ferret-badger *(Melogale moschata)*, found at low elevations and described as feeding on small birds and mammals [*13*]. I saw one at 400 meters in primary (or mature secondary) hardwood forest in the Coastal Range. Swinhoe's Pheasants were reported from the same area.

Food

Taka-Tsukasa and Kano [*22*] reported that Swinhoe's Pheasants ate insects and nuts. Later Taka-Tsukasa [*21*] wrote that the pheasants were partial to acorns of *Quercus* and to ripe berries and that by scratching with their feet they took earthworms and millipedes.

Team members clearly saw two species of plants that provided food for wild pheasants: the red berries of the shrub *Damnacanthus indicus* (Rubiaceae) and the white flower buds of the herb *Polygonum chinense* (Polygonaceae). The leaves of *Neolitsea* sp. (Lauraceae) and *Asplenium* sp. (Polypodiaceae) appeared to have been eaten, but because of distance and obstructing vegetation a clear observation could not be made.

The following genera and species of plants were reported by those interviewed as part of the diet of Swinhoe's Pheasants: *Actinodaphne* sp. (Lauraceae), *Camellia* sp. (Theaceae), *Cordia dichtoma* (Boraginaceae), *Gardenia jasminoides* (Rubiaceae), and cassava *Manihot utilissima* (Euphorbiaceae). Cassava was the one exotic cultivated plant reported to have been eaten by Swinhoe's Pheasants. They may have been feeding on the nutritious, starch-filled roots, although this was not specifically stated. Five people reported that Swinhoe's Pheasants ate seeds of the wild taro, *Alocasia macrorrhiza* (Araceae). Another informant saw two adult males feeding together on taro seeds in February. Taro is a shade-tolerant species and according to Wang [*23*] is indicative of second growth that is approaching maturity. In summary, Swinhoe's Pheasants feed on different parts of plants, including buds, berries, seeds, leaves, and possibly roots.

Little is known about the animal species which may be taken as food. Informants generally reported that pheasants ate insects, worms, and termites. One reported that pheasants ate insects in rotting logs. We saw a soft, rotting log recently picked apart, with fine white wood shavings scattered on the ground beside it. The feeding signs were attributed by our hunter-guide to Swinhoe's Pheasants. This was not verified directly, but we knew Swinhoe's Pheasants were in the area.

Summary

I surveyed wild populations of Swinhoe's Pheasants in the mountains of Taiwan from 1972 to 1974. Data were gathered from direct observations and from interviews with people who had seen or hunted them. In 1974, Swinhoe's Pheasants were still widely distributed in the mountains from close to sea level (in a few remote, undisturbed areas) up to 2,500 meters but were most common between 1,500 and 2,300 meters. A previously unreported population was discovered in the isolated Coastal Mountain Range on the Pacific coast. Since the species was discovered in 1862 by Robert Swinhoe, its range has diminished and its distribution has become disjunct due to habitat destruction and expanding human settlements. Its population has almost certainly declined as a result, but, in 1974, the pheasants probably still numbered in the thousands. Swinhoe's Pheasants prefer, and may be dependent on, primary or indigenous mature secondary hardwood forest on gentle slopes ($<40°$). There is no solid evidence to indicate that this pheasant can adapt to disturbed habitats. Survival as a species, therefore, will probably depend on the preservation of tracts of undisturbed hardwood forests.

Swinhoe's Pheasants feed on a variety of plants and plant parts and on invertebrates in the leaf litter or in rotting logs. They may also feed in areas on the forest floor cleared by the sympatric Formosan Hill Partridge, *Arborophila crudigularis*.

Wild pheasants are extremely wary. They rarely vocalize and rarely flush, habitually escaping on foot. Pheasants were more frequently seen during dry periods and retired deep in the forest during rainy periods. They were rarely seen once the sun had risen and were quite inactive during midday hours. Swinhoe's Pheasants are probably polygynous with breeding males maintaining territories. The breeding period is concentrated from March through May. Females tend to lay five to eight eggs in simple but protected depressions in the ground or in slightly elevated sites. There is strong evidence that they also nest in trees.

Man is the most serious predator. Otherwise, the most likely predator is the ferret-badger, *Melogale moschata*.

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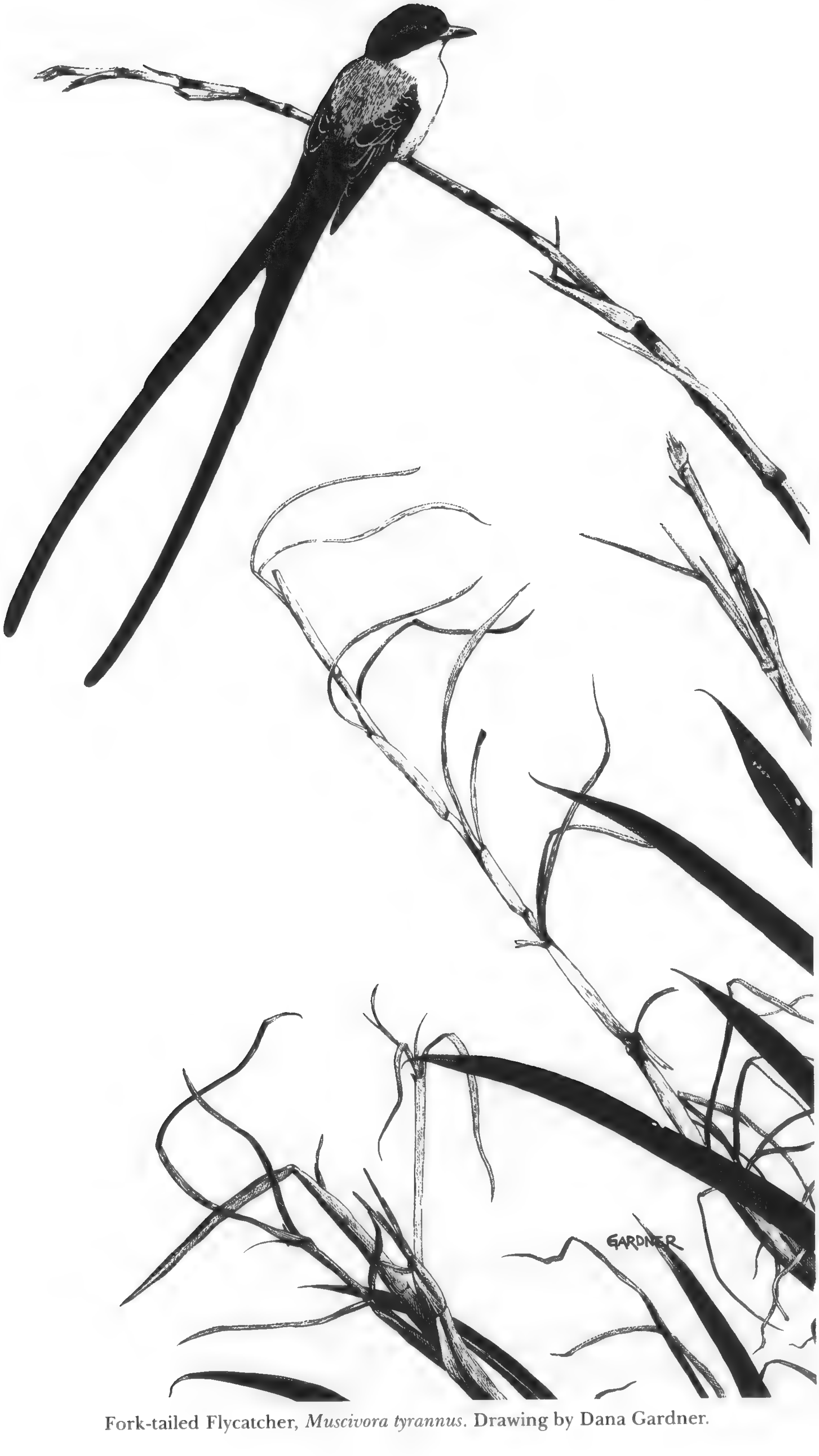

Fork-tailed Flycatcher, *Muscivora tyrannus*. Drawing by Dana Gardner.

LE CONTE'S SPARROW: A RARE STUDY FROM LIFE

ROBERT M. MENGEL

Aside from some of the rails, perhaps the most notoriously secretive and difficult North American birds to observe in life, much less sketch, are some of the "grassland sparrows," notably such "sharp-tailed" species as the Grasshopper *(Ammodramus savannarum)*, Baird's *(A. bairdii)*, Henslow's *(A. henslowii)*, Le Conte's *(Ammospiza leconteii)*, Sharp-tailed *(A. caudacuta)*, and Seaside *(A. maritima)* sparrows. Except for the mysterious Baird's Sparrow, Le Conte's may be the least frequently seen, breeding in remote taiga and northern prairie marshes, wintering in the sparsely populated prairie regions to the south, and normally showing itself only in the brief intervals between flushing and dropping back into heavy cover.

I have had my share of experiences with all of these birds except Baird's Sparrow, which has continued to elude me in life. As a young Cornell student I marvelled at George Miksch ("Doc") Sutton's skills in singling out briefly flitting migrant Sharp-tailed Sparrows from other esoteric "lbj's" in the Cayuga Lake marshes at Ithaca.

Later on I sometimes observed briefly, and occasionally collected in the line of scientific duty, various races of the Seaside and Sharp-tailed sparrows and, more frequently, Grasshopper, Henslow's, and Le Conte's, chiefly by very quick wing-shooting which is often the only way. While attempting to document the occurrence and seasons of these birds in Kentucky I learned that a low-flitting mahogany-colored wisp is a Henslow's, a bit of wind-blown straw a Le Conte's, and the much more numerous Grasshopper Sparrow is somewhere between. (Lincoln's, *Melospiza lincolnii*; Bachman's, *Aimophila bachmanii*; Savannah, *Passerculus sandwichensis*; and others are "keyed out" by subtle but generic distinctions in habitat, flight quality, and silhouette.)

But almost never, even on the comparatively rare occasions when I could watch a singing bird through binoculars, have I had real chance to draw one of these species from life in ways permitting one to see well and at length with the unaided eye. The principal exception is the subject of this reminiscence.

One night in mid-October of 1955 an unusual opportunity came to me in a most unexpected way. When I arrived early in the evening at my office in Dyche Hall on the University of Kansas campus, numerous overhead call notes had already informed me that a significant night migration of passerine birds was under way. Several hours later, with the manuscript of my "Birds of Kentucky" presumably advanced by some pages, I was aroused from somnolence, in the manner of Edgar Allen Poe, by a gentle tapping sound. This came, however, not from the door but from a window.

Investigating, far from the raven of poetry, I discovered a minute, straw-colored sparrow scurrying about on the window ledge and fluttering against the pane, evidently confused by the office lights. I opened the window and it quickly retreated along the 31-inch wide ledge until restrained by a cul-de-sac cluttered by the rearing of many generations of pigeons.

Ornithological curiosity soon overcame a healthy acrophobia and I gingerly crept out onto the ledge, four floors above the street, and crawled forward some 15 feet, concentrating very carefully on the terrain ahead. Trapping the cornered bird gently in a slightly sweaty palm, I retreated backward with even greater caution and re-entered the office. The bright-eyed midget in my hand was, of course, a Le Conte's Sparrow, somberly elegant in freshly acquired autumn (that is, Basic) plumage.

I rationalized that the bird would profit from temporary rest and restraint. Conveniently, just outside the east window wall of my home was a large, glass-fronted enclosure about four feet high by four feet wide by 18 inches deep. I fitted this with dry grass for concealment, twigs for perches, water, and an abundant supply of "wild bird seed" from the feeder and introduced the bird.

The next day was warm and pleasant. The bird spent much time more or less concealed in the grass, feeding or resting. It showed no signs of fear, however, and periodically moved about and perched in full view. I began numerous sketches in these intervals and was able in time, by shifting attention from sketch to sketch, to complete several. The accompanying study, dated 16 October 1955, is the last and best of the series that resulted.

Not surprisingly, it is immeasurably superior to various earlier studies of the same and related species necessarily based on freshly taken specimens or, worse, study skins.

Well fed, watered, and rested, the sparrow was later released in excellent condition and appropriate habitat.

I thank John William Hardy for making the original available for reproduction.

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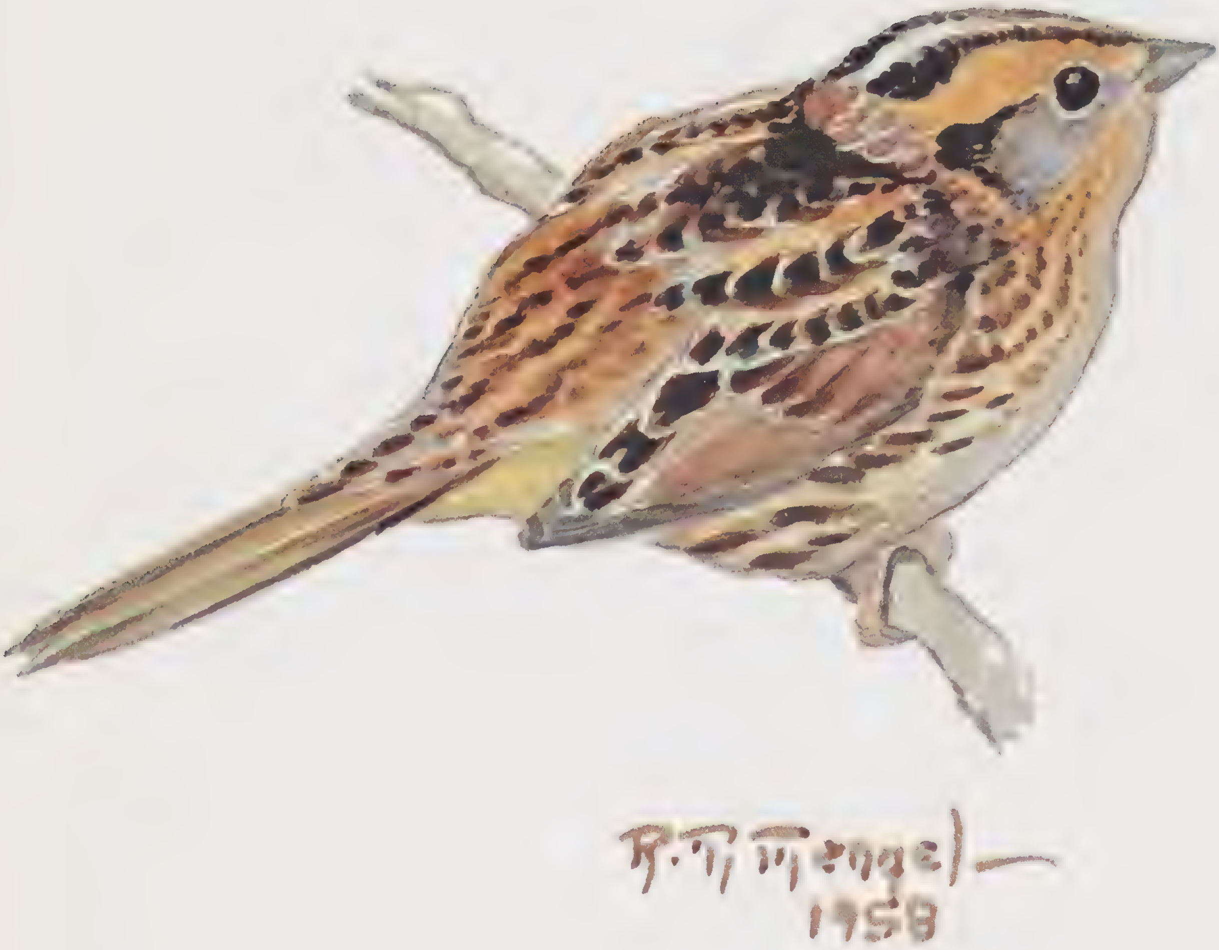
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Le Conte's Sparrow, *Passerherbulus caudacutus*. Watercolor. Painted from life by Robert Mengel.

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1969	George Miksch Sutton
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1971	Peter Scott
1972	Allan D. Cruickshank
1973	Oliver L. Austin, Jr. and Elizabeth S. Austin
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The Cornell Laboratory of Ornithology is a center for the study and cultural appreciation of birds, with headquarters in Sapsucker Woods, three miles from the main campus of Cornell University in Ithaca, New York. The Laboratory is open almost every day of the year and visitors are welcome.

A separate department within the administrative complex at Cornell University, the Laboratory is primarily concerned with scientific, educational, and cultural activities. The Laboratory is largely self-supporting, obtaining most of its funds for research and educational endeavors through gifts, grants, memberships, a home study course in bird biology, and the sale of phonograph records and cassettes, color slides, fine bird prints, and books and other printed material. Catalogues and price lists of these items may be obtained upon request from the Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850.

The Laboratory's research activities include the Data Records Programs, which gather nesting information on all colonial and non-colonial species of North American birds through the cooperation of many hundreds of observers in the United States and Canada. The program aims to provide data for the analysis of population trends, rates of survival, and other phenomena.

In another research program, biologists have developed techniques for propagating in captivity endangered raptors, such as the Peregrine Falcon, and are reintroducing them into the environment from which they have disappeared as nesting birds.

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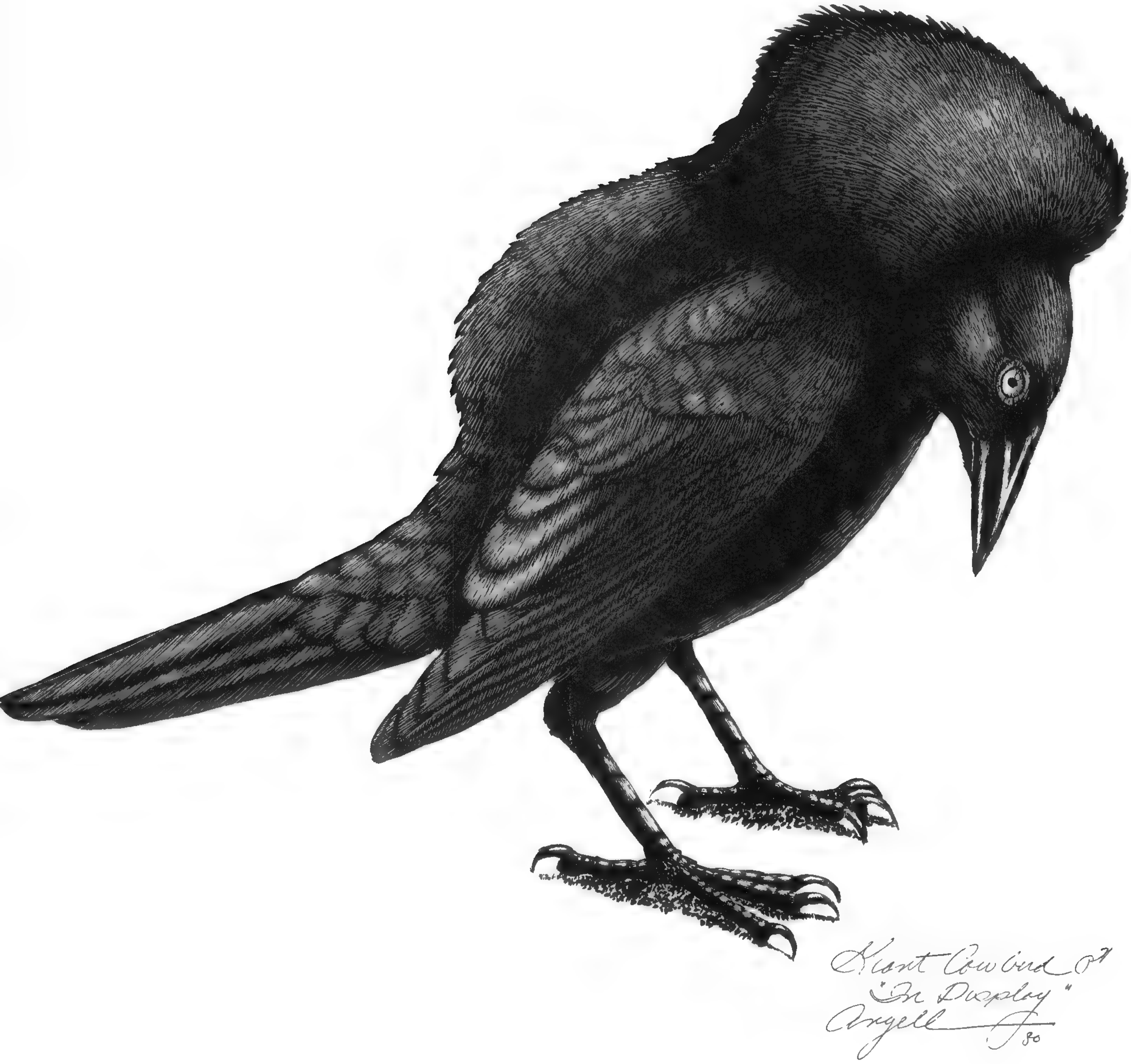
Giant Cowbird ♂
"In Display"
Angell '80

Giant Cowbird, *Scaphidura oryzivora*, displaying. Drawing by Tony Angell.